A REVIEW OF THE *AEDES SCUTELLARIS* SUBGROUP WITH A STUDY OF VARIATION IN *AEDES PSEUDOSCUTELLARIS* (THEOBALD)

(DIPTERA : CULICIDAE)

BY

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A REVIEW OF THE *AEDES SCUTELLARIS* SUBGROUP WITH A STUDY OF VARIATION IN *AEDES PSEUDOSCUTELLARIS* (THEOBALD). (DIPTERA : CULICIDAE)

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CONTENTS

SYNOPSIS

Eighteen described and three undescribed members of the *Aedes scutellaris* subgroup are recognized from the Australasian region and eastern part of the Oriental region. The systematic status accorded to members is reviewed, the diagnostic specific characters critically examined, and the geographical distribution of the subgroup illustrated and discussed.

An original pictorial chart for identification of members of the subgroup indicates also the geographical distribution of various taxonomic characters, the implications of which are considered. The general trend is from west to east but one character shows a north-south distribution. A key to adults is provided for use with the chart, and the inadequate state of present knowledge of immature stages is briefly indicated.

Source and experimental methods of rearing a colony of *Aedes pseudoscutellaris* Theobald are described. Results are tabulated of a biometrical study of twenty-eight characters, in five series of *pseudoscutellaris* adults bred from larvae whose environment had been subjected to controlled variation of either temperature or salinity, and in one series of adults from different stock, also bred in controlled conditions. The records are analyzed and their implications discussed.

The results support the specific status accorded to members of the *scutellaris* subgroup, in that the observed range of experimental variation is not generally of the same magnitude as interspecific differences in the same character. Lack of variation in the basal lobe of the male coxite is evidence of its value in defining species. Two characters should probably be used with caution for delimiting species, since *pseudoscutellaris* can exhibit both extremes of their development. A complete interruption to the white bands on hind tarsal segments II–IV can be produced by low temperatures of larval environment. Presence or absence of a white streak under the proboscis may be due to differences in hereditary constitution, though larval environment also has some effect.

I. INTRODUCTION

In recent years, many closely related mosquitoes which were, or would have been, regarded by earlier workers as varieties or subspecies, have been given full specific status. This is partly due to more adequate material being available for study, but in certain well-investigated groups, biological studies have suggested or proved the distinctness of the forms concerned, where morphological differences are slight or obscure. At the same time, cross-breding experiments have shown a few forms to be no more than subspecies. The classical example is the *Anopheles maculipennis* complex in Europe; others are the *Anopheles maculipennis* complex in North America and the *Anopheles gambiae* complex in Africa. Culicine mosquitoes have not received the same attention as Anophelines, but the *Culex pipiens* complex is now being widely studied.

All the foregoing groups of mosquitoes have a continental distribution. Where the members of a complex are geographic races, largely confined to different island groups, there might appear to be a strong case for regarding some, at least, of them as subspecies. Such a complex is the *Aedes scutellaris* subgroup, widely distributed in the Australasian region and the eastern part of the Oriental region. Of the

eighteen described members of the subgroup, seventeen have been treated by recent authors as full species ; cross-breeding experiments have involved only four members, one of which, as a result, is regarded as a subspecies. There is a little evidence indicating biological differences between sympatric members of the subgroup, but no intensive research on the subject has been made. In many cases quite small morphological differences are used to separate the species.

Huxley (1942) described variation as "... a study of the differences between organisms. On analysis, these differences may turn out to be due to differences in environment ... or ... to differences in hereditary constitution ... or ... to a simultaneous difference both in environment and in constitution ... The important fact is that only experiment can decide between the two." Simpson (1944) pointed out that "... no morphological character is inherited as such. What is inherited is a complex of potentialities for development, and the ultimate morphological expression of the same hereditary characters may differ markedly."

It appeared that some light might be shed on the systematic status of members of the *scutellaris* subgroup by a study of the amount of variation that could be induced in one member by controlled variation of the environment. Comparison of specimens from different stocks of the same species, reared in identical conditions, might indicate differences due to hereditary constitution. At the same time, the reliability of certain taxonomic characters could be tested. In order to evaluate the results of the experimental work, it was first necessary to review the *scutellaris* subgroup as a whole, and to examine the characters in use for distinguishing the species.

In addition to laboratory-reared material, these studies are based on the examination of numerous specimens in the collections of the British Museum (Natural History), London School of Hygiene and Tropical Medicine, Bernice P. Bishop Museum, Honolulu (E. C. Zimmerman collection), and University of Queensland, and on notes on specimens in the U.S. National Museum made by Dr. Alan Stone.

II. REVIEW OF THE *SCUTELLARIS* SUBGROUP

(1) *General Survey*

The subgenus *Stegomyia* Theobald of genus *Aedes* Meigen is practically confined to the tropical and subtropical regions of the old world, chiefly the Ethiopian, Oriental and Australasian regions. *Aedes* (*Stegomyia*) *aegypti* Linn. has spread to the new world by man's agency.

A group of species within the subgenus *Stegomyia* is known as the *scutellaris* group. Its exact limits have been differently interpreted.

Edwards (1932) divided the subgenus *Stegomyia* into four groups. In what he termed " Group C (*scutellaris* group) " he included ten species from the Oriental and Australasian regions, Crete and Africa. Three of these were known from the Australasian region, *A.* (*S.*) *albolineatus* (Theobald), *A.* (*S.*) *albopictus* (Skuse) and *A.* (*S.*) *scutellaris* (Walker) (of which he listed five varieties).

The *albolineatus*-complex, removed from Group C by Knight & Rozeboom (1946), was named Group E (*albolineatus* group) by Knight & Hurlbut (1949). The latter

authors divided Group C, thus modified, into three subgroups, viz.: Subgroup I, *scutellaris* s.str. Subgroup II, *albopictus*, and Subgroup III, *mediopunctatus*. The term " the *scutellaris* group " as used by Farner & Bohart (1945) and more recent authors has, in fact, referred to practically the same complex of species as Knight & Hurlbut's Subgroup I.[1]

The *scutellaris* subgroup of the present paper is synonymous with Knight & Hurlbut's Subgroup I, which the authors define as follows: " Characterized by having the more mesal portions of the abdominal tergal markings sub-basal. In addition, post-spiracular scales are lacking, the scutal longitudinal median line is relatively slender, and the pleural scale patches are arranged in two rather well-defined longitudinal bands (not true of *gurneyi*, however.)"

The following list of the species included by Knight & Hurlbut under their definition, with the addition of one species and one subspecies since described is arranged in chronological order of the date of publication of the names (as either varietal or specific). The original designation is given in parenthesis.

1. *scutellaris* Walker, 1859 (*Culex scutellaris*).
2. *pseudoscutellaris*[2] Theobald, 1910 (*Stegomyia pseudoscutellaris*).
3. *tongae* Edwards, 1926 (*Aedes variegatus* var. *tongae*).
4. *andrewsi* Edwards, 1926 (*Aedes variegatus* var. *andrewsi*).
5. *alorensis* Bonne-Wepster & Brug, 1932 (*Aedes* (*Stegomyia*) *variegatus* var. *alorensis*).
6. *horrescens* Edwards, 1935 (*Aedes* (*Stegomyia*) *scutellaris* var. *horrescens*).
7. *gurneyi* Stone & R. Bohart, 1944 (*Aedes* (*Stegomyia*) *gurneyi*).
8. *marshallensis* Stone & R. Bohart, 1944 (*Aedes* (*Stegomyia*) *marshallensis*).
9. *guamensis* Farner & R. Bohart, 1944 (*Aedes* (*Stegomyia*) *guamensis*).
10. *pernotatus* Farner & R. Bohart, 1944 (*Aedes* (*Stegomyia*) *pernotatus*).
11. *quasiscutellaris* Farner & R. Bohart, 1944 (*Aedes* (*Stegomyia*) *quasiscutellaris*).
12. *hensilli* Farner, 1945 (*Aedes* (*Stegomyia*) *hensilli*).
13. *paullusi* Stone & Farner, 1945 (*Aedes* (*Stegomyia*) *paullusi*).
14. *riversi* R. Bohart & Ingram, 1946 (*Aedes* (*Stegomyia*) *riversi*).
15. *scutoscriptus* R. Bohart & Ingram, 1946 (*Aedes* (*Stegomyia*) *scutoscriptus*).
16. *hakanssoni* Knight & Hurlbut, 1949 (*Aedes* (*Stegomyia*) *hakanssoni*).
17. *scutellaris katherinensis* Woodhill, 1949 (*Aedes scutellaris katherinensis*).
18. *polynesiensis* Marks, 1951 (*Aedes* (*Stegomyia*) *polynesiensis*).

[1] *A.* (*S.*) *gurneyi* is often placed with *albopictus*; *scutoscriptus* is also aberrant. Stone & Farner (1945) found *A.* (*S.*) *galloisi* Yamada difficult to place, from the description, and omitted it from their key; Knight & Hurlbut (1949) place it in Subgroup II, *albopictus*.

[2] Marks (1951) demonstrated that two species had previously been confused under the name " *pseudoscutellaris*." In this paper " *pseudoscutellaris* " is used for authors' references which do not discriminate between the two forms. Where the identity of the form is beyond doubt it is referred to under the appropriate name *pseudoscutellaris* or *polynesiensis*.

In addition there are three other forms known but not named.[1] The form of *A.* (*S.*) *scutellaris* described from Andaman Is. by Barraud (1928, 1934) is recognized by recent authors as probably distinct, and from my own observations of specimens I feel satisfied that this is so. Edwards (1929) noted a form from Rotuma I., north of Fiji, which differed in certain aspects from "*pseudoscutellaris*." I have seen this also and it appears to represent a distinct race. Both these forms await review when more adequate material is available. Bohart & Ingram (1946*b*) gave some details of "*Aedes* sp. in *scutellaris* group" from Palau Group, Caroline Islands, and Dr. Alan Stone (*in litt.*) considers it is a valid species. He has sent me additional particulars of it which confirm his finding.

The *scutellaris* subgroup is equivalent to a "species group" of Zeuner (1943), or to a "superspecies" of Mayr (1942), if the latter concept were modified, as seems reasonable, to include groups of species which are mainly allopatric but in which the ranges of a few species overlap.[2]

Mattingly (1953) considers that *A.* (*S.*) *granti* (Theobald), which Knight & Hurlbut (1949) placed in Group C, Subgroup II—*albopictus*, belongs to the *scutellaris* subgroup, which it resembles in pleural markings. Mattingly uses the presence of an extra stripe of pale scales between the dorsal border of the sternopleuron and the lower edge of the posterior pronotum to link *granti* with *hakanssoni* and *scutoscriptus*, and to distinguish them from "more typical members of the group." However, a similar stripe may occur in *scutellaris*, in *pseudoscutellaris* and, reduced in length, in *polynesiensis*. It is most likely to be seen in large unrubbed specimens and might well be found in other species if suitable series were available. Descriptions indicate that *granti* differs from all the species here included in the *scutellaris* subgroup in markings of proboscis, female palps, wings, legs, scutellum and abdominal tergites (which have the white bands basal medially). While some species of the subgroup do not conform in certain characters with the general pattern, there is an overall strong indication of close relationship. In my opinion, inclusion of *granti* would destroy the homogeneity of the subgroup, which could no longer be regarded as representing a superspecies, whereas, if *granti* were placed by itself in a separate subgroup of Group C, the affinities with the *scutellaris* subgroup indicated by the pleural pattern would not be obscured.

The full synonymy of the various species of the *scutellaris* subgroup, first dealt with by Edwards (1917), has been fully covered in recent papers on the group (1944 onwards), and finally cleared up by the examination of a topotypic male of *Aedes scutellaris* (Walker). by Stone (1947). In references to earlier papers, species are treated here under the names by which they are at present recognized.

Table I records the treatment which species described before 1940 have received

[1] Since this paper went to press, Dr. R. M. Bohart has informed me of a fourth undescribed species from Korror I., in the Palau Group, and has very kindly supplied details which will enable it to be distinguished from others in the subgroup. Descriptions of the two species referred to here as Palau sp. and Korror sp. will be published by Dr. Bohart at an early date. In addition Mr. Mattingly informs me that he has recently examined a specimen of the *scutellaris* subgroup from the Maldive Is., a description of which is in the press. In the majority of characters, including the basal lobe of the male coxite, it closely resembles *scutellaris scutellaris* but it differs in having white scales on the under side of the proboscis.

[2] The concept has recently been so modified (Mayr et al., 1953, p. 29).

TABLE I.—*Synopsis of Taxonomic Status Accorded Members of the* scutellaris *Subgroup described before 1940*

Species and synonyms	Theobald (1901)	Edwards (1917)	Edwards (1924)	Edwards (1926)	Bonne-Wepster and Brug (1932)	Edwards (1932)
Scutellaris . . .	*Stegomyia scutellaris*			*A.* (*S.*) *variegatus*	*A.* (*S.*) *variegatus*	*A.* (*S.*) *scutellaris*
Culex variegatus Doleschall (*nec* Schrank), 1858						
Culex zonatipes Walker, 1861	Syn. of *Stegomyia fasciata* (Fabr.) (= *A.* (*S.*) *aegypti* Linn.)	*Stegomyia variegata*	*Aedes* (*Stegomyia*) *variegatus*			
Aedes variegatus var. *hebrideus* Edwards, 1926				*A.* (*S.*) *variegatus* var. *hebrideus*	*A.* (*S.*) *variegatus* var. *hebrideus*	*A.* (*S.*) *scutellaris* var. *hebrideus*
Pseudoscutellaris . .	(1910) *Stegomyia pseudo-scutellaris*			*A.* (*S.*) *variegatus var. pseudo-scutellaris*	*A.* (*S.*) *variegatus var. pseudo-scutellaris*	*A.* (*S.*) *scutellaris* var. *pseudoscutellaris*
Tongae . . .	—	—	—	*A.* (*S.*) *variegatus* var. *tongae*	*A.* (*S.*) *variegatus* var. *tongae*	*A.* (*S*) *scutellaris* var. *tongae*
Andrewsi . . .	—	—	—	*A.* (*S.*) *variegatus* var. *andrewsi*	*A.* (*S.*) *variegatus* var. *andrewsi*	*A.* (*S.*) *scutellaris* var. *andrewsi*
Alorensis . . .	—	—	—	—	*A.* (*S.*) *variegatus* var. *alorensis*	—
Horrescens . . .	—	—	—	—	—	—

Varieties

Species and synonyms	Barraud (1934)	Edwards (1935)	Knight, Bohart & Bohart (1944)	Farner & Bohart (1945)	Stone & Farner (1945)	Bohart & Ingram (1946)	Stone (1947)
Scutellaris . .	*A.* (*S.*) *scutellaris*	—	*A.* (*S.*) *scutellaris scutellaris*	—	*A.* (*S.*) *scutellaris*	—	*A.* (*S.*) *scutellaris*
Culex variegatus Doleschall (*nec* Schrank), 1858							
Culex zonatipes Walker, 1861							
Aedes variegatus var. *hebrideus* Edwards, 1926 .	*A.* (*S.*) *scutellaris* var. *hebrideus*	—	*A.* (*S.*) *scutellaris hebrideus*	*A.* (*S.*) *hebrideus*	*A.* (*S.*) *hebrideus*	*A.* (*S.*) *zonatipes*	
Pseudoscutellaris .	*A.* (*S.*) *scutellaris* var. *pseudoscutellaris*	—	*A.* (*S.*) *scutellaris pseudoscutellaris*	*A.* (*S.*) *pseudo-scutellaris*	*A.* (*S.*) *pseudo-scutellaris*	*A.* (*S.*) *pseudo-scutellaris*	
Tongae . . .	*A.* (*S.*) *scutellaris* var. *tongae*	—	*A.* (*S.*) *scutellaris tongae*	*A.* (*S.*) *tongae*	*A.* (*S.*) *tongae*	—	—
Andrewsi . .	*A.* (*S.*) *scutellaris* var. *andrewsi*	—	—	—	*A.* (*S.*) *andrewsi*	—	—
Alorensis . .	*A.* (*S.*) *scutellaris* var. *alorensis*	—	—	—	*A.* (*S.*) *alorensis*	—	—
Horrescens . .	—	*A.* (*S.*) *scutellaris* var. *horrescens*	*A.* (*S.*) *scutellaris horrescens*	*A.* (*S.*) *horrescens*	*A.* (*S.*) *horrescens*	—	—
	Varieties		Subspecies		Species		

from those authors responsible for changes in nomenclature or systematic status. Forms described since 1940 have suffered no change in the status ascribed to them by their original authors.

The first recognition of the *scutellaris* subgroup as such (i.e., that *A. scutellaris* as then recognized comprised a complex of closely related forms was by Edwards (1926), prompted by Buxton & Hopkins who had observed constant differences between the anal gills of larvae from Samoa and from the New Hebrides. He found that " there are at least five distinct varieties distinguishable by small differences of colour and also by the male hypopygium, especially in the form of the basal lobe of the sidepiece. The characters are fairly well defined, but are perhaps best treated as varietal rather than specific, especially as their significance appears to be mainly geographical."

Barraud (1928), Edwards (1929) and Bonne-Wepster & Brug (1932) gave details of forms from Andaman Is., Rotuma I. and Taroena (= *paullusi*) respectively which differed from those already described but did not give them varietal names ; the last authors, however, described a sixth variety, *alorensis*.

Following Edwards, varietal status was ascribed to the named forms until Knight, Bohart & Bohart (1944) listed them as subspecies, without comment on the change.

Farner & Bohart (1945) on the basis of male genitalia differences, regarded the known Australasian members of the *scutellaris* subgroup as separate and distinct species occupying similar ecologic niches. The occurrence of more than one from the same area lent support to their contention.

Farner (1945) observed, in describing *hensilli*, that it was possibly a subspecies of *guamensis* but until further material was available and in view of the differences in tarsal and abdominal banding it seemed best to regard it as specifically distinct from *guamensis*.

Since 1944, most authors have described new forms as full species without comment on their status. The exception is *scutellaris katherinensis* to which Woodhill (1949*a*) gave subspecific rank on the grounds of its ability to hybridize with *scutellaris scutellaris*.

The description in recent years of many new forms in the *scutellaris* subgroup reflects an increase in the quantity and quality of collections, and the examination of males from localities whence only females were known before. Additional characters have been brought into use for identifying the different species but it cannot be said that the recognition of the various forms as full species is due to the discovery of new and more significant characters. They are still distinguished from one another chiefly by differences previously in use for separating those forms recognized as varieties. It is the significance placed on these characters by taxonomists that has altered.

The treatment of the different forms (except *s. katherinensis*) as full species is now general, and will probably remain so unless it can be proved incorrect. Not all culicidologists are convinced that this treatment is in all cases justified, and where forms replace one another geographically it may yet be possible to demonstrate that some are, in fact, only subspecies. Morphological differences between some species appear to be no greater than those between the subspecies *s. scutellaris* and

s. katherinensis. However, to quote Mayr (1942), "Considerably more material must be examined in order to recognize subspecies, than is needed for the description of good species."

It may be, on the other hand, that, with further knowledge of geographical variation, what is now recognized as a single monotypic species will be broken up into two or more subspecies. Bohart & Ingram (1946*b*), for instance, found that specimens of *hensilli* from Ulithi had the last tarsal segment usually about half white, whereas in Truk specimens it varied from two-thirds white to all white; there was also a greater tendency for complete abdominal bands in Truk females. There may be some slight differences between *tongae* from Tonga and from Sikiana in degree of development of specialized setae on the basal lobe of the male coxite.

I have seen a series of eight specimens of *s. scutellaris* from Admiralty Is., two of which are normal, four have a line of white scales on the anterolateral margin of the scutum, one has hind tarsal V with a dark patch at the tip, and one has hind tarsal bands reduced in width and segment V dark on the apical half. A male similar to the last and a normal male were reared from the same larval collection from Aneityum I., New Hebrides, by Dr. Marshall Laird. Male genitalia of the three types appear identical. These variations have not been recorded from elsewhere in the range of *s. scutellaris*. Male genitalia of the three types appear identical.

The few hybridization experiments recorded, viz.: *s. scutellaris* × *s. katherinensis* (Woodhill, 1949*a*), *s. scutellaris* and *s. katherinensis* × *pseudoscutellaris* [1] (Woodhill, 1950), and *s. scutellaris* × *pernotatus* (Perry, 1950), have only served to confirm the status already ascribed to the forms concerned.[2] Smith-White (1950) discussed the genetical significance of non-reciprocal fertility between *s. scutellaris* and *s. katherinensis* and suggested further lines of investigation.

(2) *Taxonomic Characters*

(*a*) General

Doleschall (1858) and Walker (1859, 1861) made no comparison with other species in their descriptions, which all apply to *s. scutellaris*.

Theobald (1901, 1903, 1907, 1910*a*) included specimens of both *albopictus* and members of the *scutellaris* subgroup in his concept of *scutellaris*. When (1910*b*) he described *pseudoscutellaris* he distinguished it by the characters in which it differs from what he called "*scutellaris*", but we now know to have been *albopictus*, i.e., by the typical *scutellaris* subgroup pleural markings of white lines. He also observed the curving white lateral patches on the abdominal tergites. Edwards (1917) included several forms of the *scutellaris* subgroup, among them *pseudoscutellaris*, in one monotypic species and it was not until 1926 that he realized they represented a complex of distinct forms.

[1] I have confirmed by examination of specimens the identity of Woodhill's colony as *pseudoscutellaris* and not *polynesiensis*.

[2] Woodhill (1954) has crossed *pseudoscutellaris* from Fiji with *polynesiensis* from Tahiti and obtained small numbers of fertile hybrids, showing that the two species are not genetically isolated, though they do not mate readily in laboratory conditions. This suggests that *polynesiensis* may be a subspecies of *pseudoscutellaris*. However, repetition of the experiment using Fijian *polynesiensis* and a study of the habits of the two forms, where they occur together in nature, would appear desirable in order to judge whether there are barriers to their natural hybridization.

The characters discussed here include all that have been found of importance by Edwards and later authors in identification of specimens of the *scutellaris* subgroup and some which have been suggested but are not in general use. A consideration of their occurrence and variability supplements the information given in Plate 1. They do not, however, include all characters which may be noted in descriptions. The first author to use a character is indicated. A name is put in inverted commas where it is obvious that an author was including more than one form under it.

Colour differences have been noted in some cases. Not enough is known about factors causing differences in scale colour, but generally in mosquito taxonomy, such small differences as between white and creamy white or yellowish are of doubtful value.

(*b*) Head

Bonne-Wepster & Brug (1932) noted in the median white stripe on the vertex, a difference in the width towards the nape between "*scutellaris*" and *alorensis*; this character is not in general use.

The same authors observed that Taroena specimens of "*scutellaris*" (= *paullusi*) had a distinct white line under the proboscis; this feature is now known to occur in a number of species, sometimes in the male only; in some cases it appears to be very variable.

Stone & Farner (1945) noted the white stripe in *paullusi* males, but only a few pale scales under the female proboscis; I have seen a male of this species from Samar I. which lacks the white stripe. The following species have a white stripe: *riversi* ♂, ♀; *quasiscutellaris* ♂, ♀; *tongae* ♂, ♀ (Stone & Farner (1945) observed this in ♂, it is also present in all ♀♀ I have seen); *horrescens* ♂ (♀ with some pale scales); *pernotatus* ♂, ♀ (but I have seen *pernotatus* ♂♂ in which it was lacking). It is present also but has not previously been noted in Andamans sp. ♂, ♀, and *alorensis* ♂; and I have observed that there may be some pale scales under the proboscis in *andrewsi* ♂, *scutoscriptus* ♂ (Dr. Alan Stone informs me (*in litt.*) that *scutoscriptus* has a faint line of yellowish brown scales on the underside of the proboscis) and Rotuma sp. ♂. Bohart & Ingram (1946*b*) noted that the proboscis of "*pseudoscutellaris*" ♂♂ sometimes has some pale scales beneath; this was also observed by Marks (1951*a*) in "*pseudoscutellaris*" (= *polynesiensis*) ♂♂ and ♀♀. Both sexes of *pseudoscutellaris* may have proboscis with a white stripe beneath, or entirely dark; variation in this is shown in Table V.

Stone & Bohart (1944) found that *marshallensis* had the white markings on the male and female palps considerably reduced; this is the only species thus distinguished.

(*c*) Thorax

Scutum. Edwards (1926) noted that the scales of the median stripe might be creamy rather than white. Bonne-Wepster & Brug observed that the stripe in *alorensis* was narrower than in "*scutellaris*," and Edwards (1935) that in *horrescens* it was broader than in "*pseudoscutellaris*" but no measurements have been made

from comparable series of different species. Environmental conditions can affect this character in *pseudoscutellaris*.[1] The median line often continues into a denfiite or faint fork on either side of the prescutellar bare area: Bonne-Wepster & Brug (1932) noted some whitish scales in this position in "*scutellaris*," a distinct fork occurs in *hakanssoni* and *scutoscriptus*, and I have observed it also in Andaman Is., form and in *alorensis*; Woodhill (1949*a*) found no fork in the great majority of specimens of *s. katherinensis*; most authors refer to it only in general terms. Variation of the amount of white scaling in this position in *pseudoscutellaris* is shown in Table VII. It may be a character of which more use could be made.

Bonne-Wepster & Brug (1932) observed a narrow white line on the anterolateral margin of the scutum in Taroena specimens of "*scutellaris*" (= *paullusi*); Stone & Farner (1945) observed a similar line of fine yellowish scales in *quasiscutellaris* (not noted in the original description); *scutoscriptus* has a broad line in this position; a narrow line occurs in *hakanssoni*, *pseudoscutellaris*, and in some specimens of *s. scutellaris* from Admiralty Is. In all except probably *scutoscriptus* these lines are variable and may be incomplete, particularly in females. In *pseudoscutellaris* they may be reduced to patches of scales on the scutal angles. Species which usually have the scutal angle dark scaled may sometimes have two or three pale scales in this position though this has not been recorded in descriptions. I have observed this in *polynesiensis*, *andrewsi*, *alorensis*, *guamensis*, *horrescens* and Rotuma sp. The number of pale scales on the scutal angle is important in distinguishing between specimens of *pseudoscutellaris* and *polynesiensis* and would possibly prove of use in other cases if details were available.

The white scales above the wing root are usually all broad. In *hakanssoni* this is not specifically stated in the description and, in fact, I have observed that they are mainly narrow-curved. In *scutoscriptus* there are some narrow-curved scales in addition to the broad ones noted in the description. It is possible that they have been overlooked in other species also, and it is a character that is worth further investigation.

Scutellum.

The characteristic scaling of the scutellum in the *scutellaris* subgroup is white, with a small patch of black scales at the apex of the midlobe. Knight & Hurlbut (1949) found that *hakanssoni* has much more extensive black scaling. *Gurneyi* is described on differences from *albopictus* and by inference has all lobes entirely white scaled, but Dr. Stone informs me (*in litt.*) that there are a few dark scales at the tip of the midlobe in unrubbed specimens.

Pleuron.

Stone & Bohart (1944) observed that the white scales on the pleura of *gurneyi*

[1] Mr. P. F. Mattingly drew my attention to a character which Edwards found useful in separating African species of *Stegomyia*, viz., the presence of broad scales medially on the anterior margin of the scutum. A cursory examination of the experimental series of *pseudoscutellaris* showed that these scales might be present or absent and suggested that they are affected by environment though this was not thoroughly investigated. The character therefore does not appear a promising one for use in the *scutellaris* subgroup.

are arranged in patches rather than the straight lines characteristic of other members of the *scutellaris* subgroup (in this it resembles *albopictus*). The description of *scutoscriptus* indicates that only the upper pleural line is complete in this species.

Specimens of some species have the upper and lower white patches on the mesepimeron fused, in others they are separate; usually no note of this is given. I have observed both conditions in *pseudoscutellaris* and it does not appear a promising diagnostic character, though it would need further investigation to be certain.

Wings. These are dark scaled in all species. Wing length is often given as a measure of size but not as a diagnostic character. In some species a white spot occurs at the base of the costa; it has possibly been overlooked in others; it is a practically constant character in *pseudoscutellaris*. The ratio of the length of the fork cells to their stems, a character used in several culicine groups, is omitted from most descriptions.

Halteres. The scaling of the halteres is not recorded for all species, but in most the knob appears to be mainly dark scaled, whereas in *scutoscriptus* Farner & Bohart (1946) observed it to be entirely pale scaled and in *hakanssoni* it is largely pale.

(*d*) Legs

Fore femur. Stone & Bohart (1944) noted the absence of a white apical spot on the fore femur of *marshallensis* but it apparently occurs in all other species.

Mid femur. Bonne-Wepster & Brug (1937), who had a mixed collection of "*scutellaris*," observed that sometimes the mid femur had a thin longitudinal white stripe on the outer (= anterior) side. Stone & Farner (1945) noted this as one of the diagnostic characters of *paullusi*; Woodhill (1949*a*) found that it was a constant character by which *s. katherinensis* could be distinguished from *s. scutellaris*. I have found that a similar white stripe occurs in *alorensis*; this had previously been overlooked. Of five adults of *andrewsi* examined, one female had an anterior line on the basal two-thirds of one femur; possibly this was an aberrant specimen, or else in this species the character may be variable.

Fore and mid tibiae in some species have scattered pale scales posteriorly, but this has not been used as a diagnostic character.

Fore and mid tarsi. Most species have white patches at the base of segments I and II on fore and mid tarsi. Edwards (1935) noted that *horrescens* had white scales more frequently on fore and mid tarsal III than did "*pseudoscutellaris*"; Farner & Bohart (1944) found that males of *guamensis* had the fore tarsus entirely dark and distinguished *pernotatus* by the presence of basal patches on III and sometimes IV and V; *quasiscutellaris* is similar to *horrescens*. I have observed that in *andrewsi* only fore and mid tarsal segment I has a basal white patch. The development of this character in *pseudoscutellaris* is shown in Table VIII.

Hind femur. Edwards (1926) noted differences in the size of the white spot at the tip of the hind femur, but this is not a useful character. Bohart & Ingram (1946*b*) drew attention to two distinct types of pattern in the marking of the anterior surface of the hind femur; there is a longitudinal pale area which either forms a tapered white line (in most species), or trails off ventrally towards the tip rather

than tapering to a sharp point (in *guamensis*,[1] *scutoscriptus*, *hakanssoni* and sp. from Palau, also in some specimens of *marshallensis* (see p. 382)).

I have observed an apparent difference between *pseudoscutellaris* and *polynesiensis* in the distance from the base of the femur to the beginning of the dark ventral scaling, but the character needs further investigation.

Hind tarsi. The white bands on the hind tarsi are one of the most important distinctive characters, and are usually measured in terms of the ratio of the length of the band to the total length of the segments ; most species have V entirely white. Edwards (1926) observed differences in the widths of the bands and gave ratios for segment IV. Bonne-Wepster & Brug (1932) observed that in " *scutellaris* " the band on I was incomplete (i.e., interrupted by dark scales beneath) and gave ratios for the bands on II–IV, noting that Taroena specimens (= *paullusi*) had wider bands on IV. Stone & Bohart (1944) found *marshallensis* had V dark on the apical half or more ; *hakanssoni* is similar ; in *hensilli* the character shows geographical variation, Ulithi specimens have the apical half dark, whereas in Truk specimens not more than one-third is dark and the segment may be all white. Two specimens of *s. scutellaris* (one from Admiralty Is. ; one from Aneityum I., New Hebrides) have been seen with apical half of V dark and bands on other segments reduced.

Farner & Bohart (1944) observed that *guamensis* had the white bands completely interrupted by dark scales on the inner side. Stone & Farner (1945) noted that *andrewsi*[2] had the bands on IV interrupted on the dorsal surface, but this appears to be variable and I have seen two females with the band quite complete. The majority of species have the band on I interrupted beneath though it is recorded as complete in a few and not noted in others. It was complete in specimens of *alorensis* and Andamans sp. examined. In some species the extent to which the remaining bands are interrupted has been found to be quite variable. *Tongae* was previously recorded as having complete bands on II–IV, but I have seen one specimen from Tonga with I–V, another with IV and V, and one from Sikiana with IV completely interrupted. Complete bands are also recorded for *pernotatus* but a specimen from Aneityum I., New Hebrides, has the bands on I–IV completely interrupted beneath. Variation in this character in *pseudoscutellaris* is shown in Tables XIII–XVIII. Farner (1945) gave measurements of the inner as well as the outer lengths of the white bands in *hensilli*. Stone & Farner (1945) reversed the usual convention by giving the width of the dark band on segment IV at its widest dimension, but no other authors have followed this formula.

(*e*) Abdomen

The characteristic markings of the abdominal tergites in the *scutellaris* subgroup are lunate lateral white patches curving away from the base of the segment into forwardly directed hooks which may extend dorsally to form a broken or complete sub-basal band across the segment. The characteristic markings of a species usually show best on tergites IV–VII but may be found on II and III in some.

[1] Not noted in the original description.

[2] Stone & Farner said they had not examined specimens of *andrewsi* and it was included in their key on the basis of the original description ; however, the latter does not mention this character.

Edwards (1926) observed the degree of completeness of these bands on the different segments of the abdomen; this continues to be one of the principal diagnostic characters employed, but in some species is rather variable. He noted the distance the bands were removed from the bases of the tergites; Bonne-Wepster & Brug (1932) also used this character, and Knight & Hull (1952) found differences in it between *paullusi* and *s. scutellaris*. It is possible that if long series of other species were examined and the measurement could be made from the actual base of the tergite, and not from the apex of the preceding one, distinctive differences might be found. In practice, with dried specimens which have been in various conditions and ages when killed and have shrunk to different extents, the character has not been proved a generally useful one, the more so as not all authors have noted it when describing species. Edwards (1926) also noted whether the lateral patches were creamy or white and (1935) on what segments they were visible dorsally; the latter character is rather unreliable. Farner & Bohart (1944) observed sub-basal lateral patches on *guamensis* which are not of the typical lunate shape, but rather triangular. There is possibly some variation in the shape of the lateral patches in other species, but no long enough series have been examined to be sure of this.

Edwards (1926) recorded the scale pattern of the sternites, whether those of the basal segments were all white, or had apical black bands; the latter is the more common condition. This is not one of the principal diagnostic characters but might be used to supplement them in some cases. It may prove rather variable and in dried specimens the sternites are often difficult to see. Some ♀♀ of *s. katherinensis* which have narrow sub-basal white bands on sternites V and VI and a submedial band on VII appear distinct from *s. scutellaris* which usually has wide basal bands on V and VI, and often only small lateral patches on VII; other specimens are much more like *s. scutellaris*.

(*f*) Male genitalia

Edwards (1926) first recognized that members of the *scutellaris* subgroup ("races of *Aedes variegatus*") could be distinguished "by the male hypopygium, especially in the form of the basal lobe[1] of the sidepiece." The parts that have been used in distinguishing members of the *scutellaris* subgroup include the ninth tergite, coxite, style and basal lobe of coxite. The complete genitalia of *pseudoscutellaris* are illustrated in Fig. 1. There are various terminologies in use for the description of the parts of the male genitalia. That followed here is given by Edwards (1941), and all except direct quotations from other authors have been translated to these terms. The male genitalia of the mosquito rotate 180° during the first 24 hours

[1] The term basal lobe is in general use for this structure in subgenus *Stegomyia*; it bears no resemblance to, for instance, the basal lobe in subgenus *Ochlerotatus*. In the *scutellaris* subgroup, its anatomical position indicates that it is homologous with the harpago (claspette of Edwards) of *Ochlerotatus* and *Finlaya*, though it lacks the terminal appendage present in those subgenera. Edwards (1941) in his general description of mosquito genitalia describes the basal lobe as a modification of the coxite on the area between the ventral root and the midsternal connection of the coxites. "In some genera part or the whole of this basal lobe has more the form of a subsidiary appendage, which has been called the claspette." In his description of subgenus *Stegomyia* he says "claspettes in the form of a hairy basal lobe or plaque attached to sternal side of coxite, this plaque in a few species with the inner part forming a small process bearing modified bristles." This is in contrast to his earlier (1932) description of the subgenus "... basal lobe (plaque) present and hairy; no claspettes."

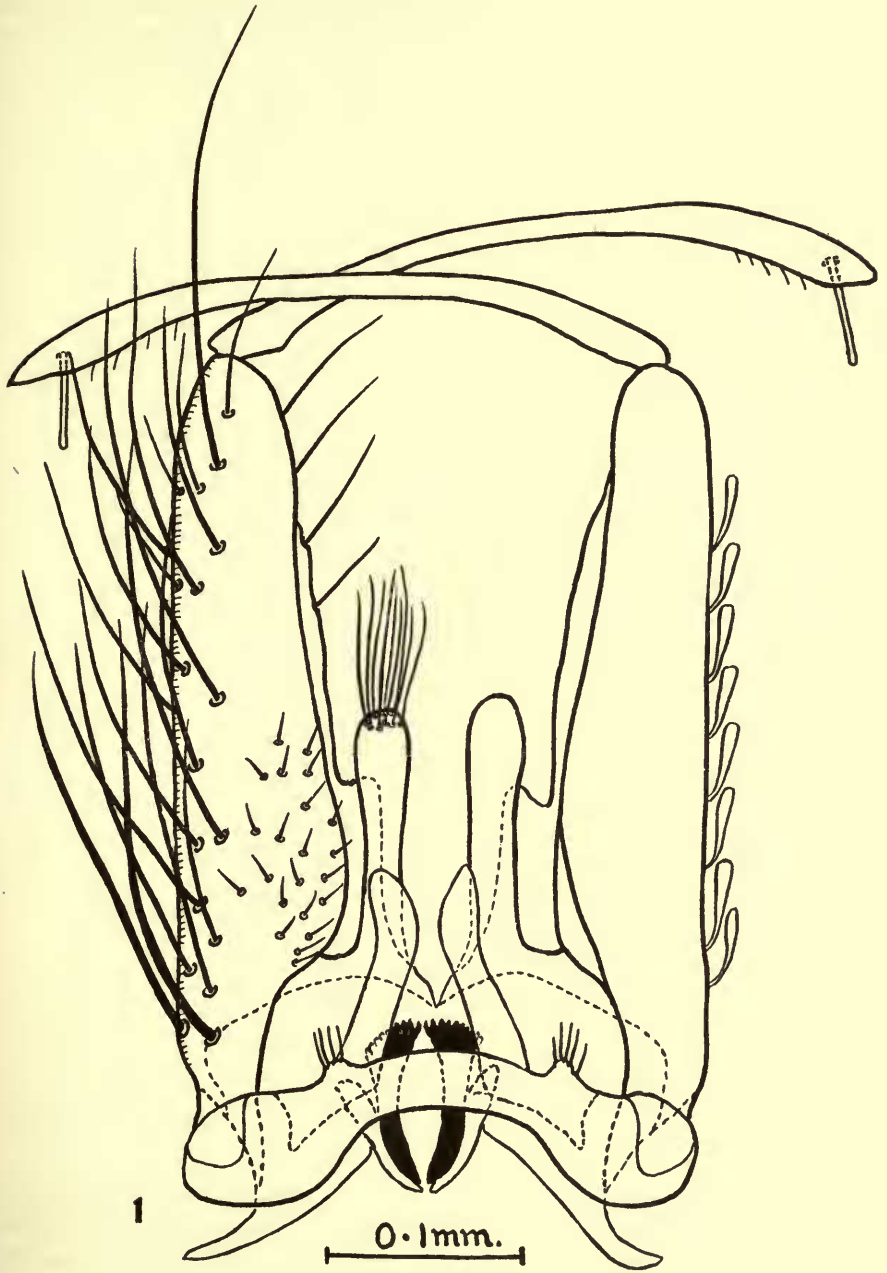


Fig. 1.—♂ Genitalia of *Aedes pseudoscutellaris* (Theobald), complete, tergal view (E. 7).

after emergence. Thus the 8th and 9th tergites become ventral, the 8th and 9th sternites dorsal. The ventral aspect referred to in the literature is therefore tergal. The left coxite, of which the basal lobe is usually illustrated, is that on the left side of the insect after rotation and therefore on the left side of figures of whole mounts

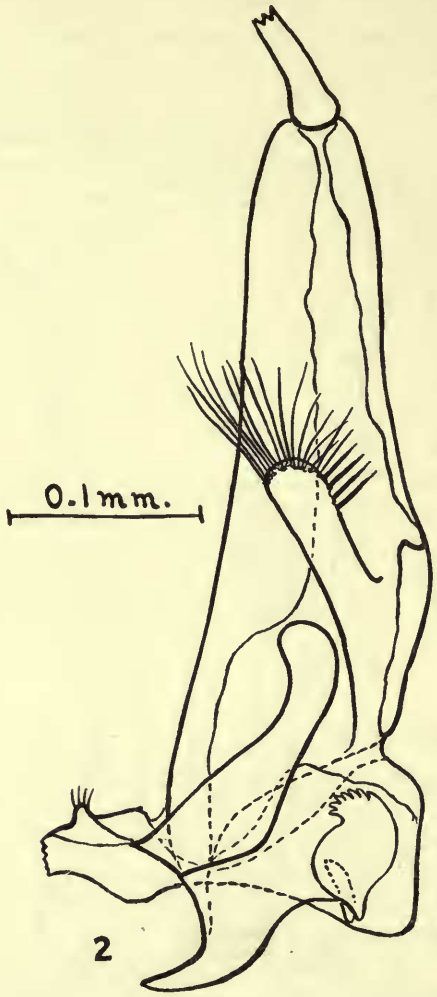
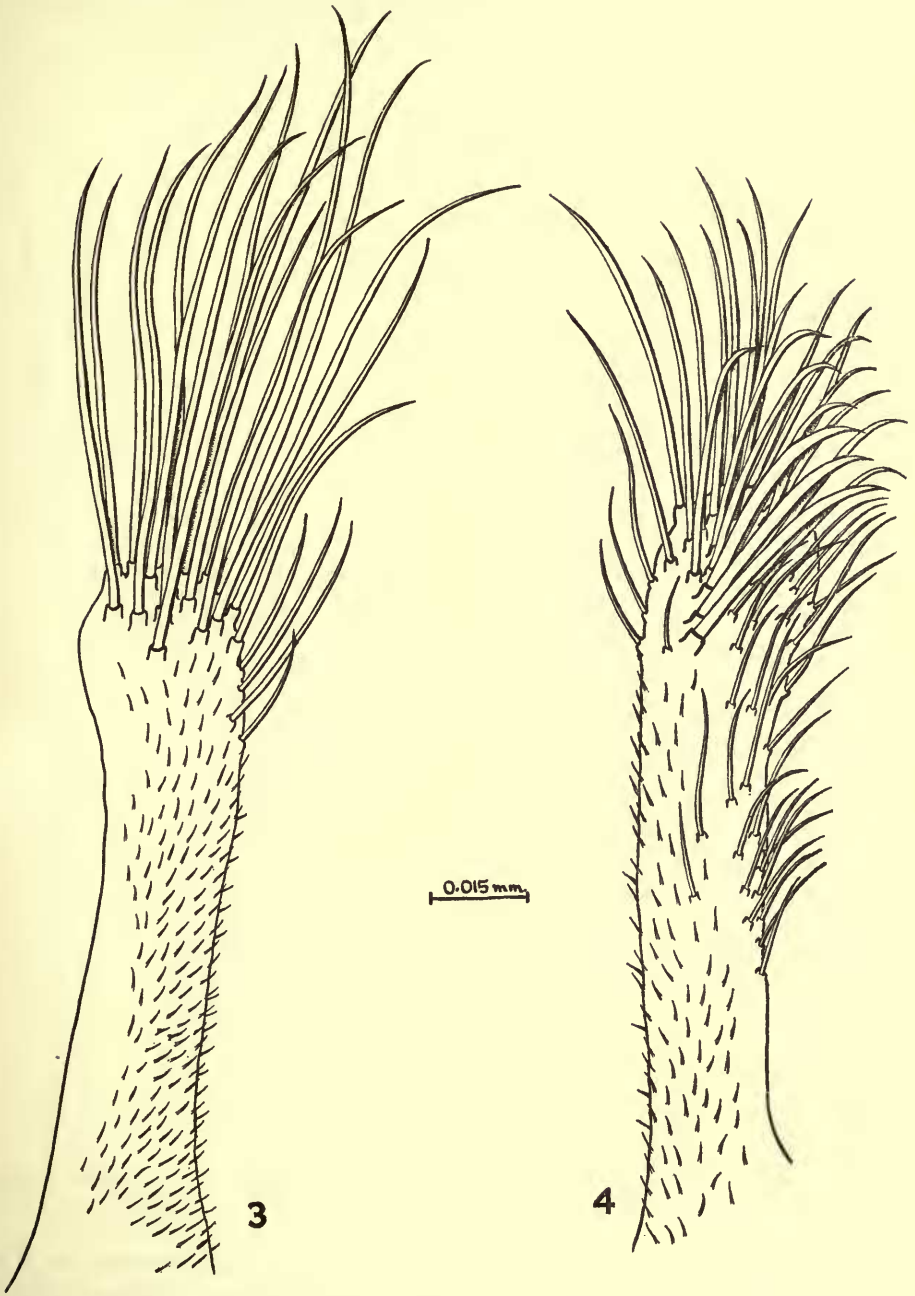


Fig. 2. ♂ genitalia of *Aedes pseudoscutellaris* (Theobald) bisected, inner lateral view (H. 33).

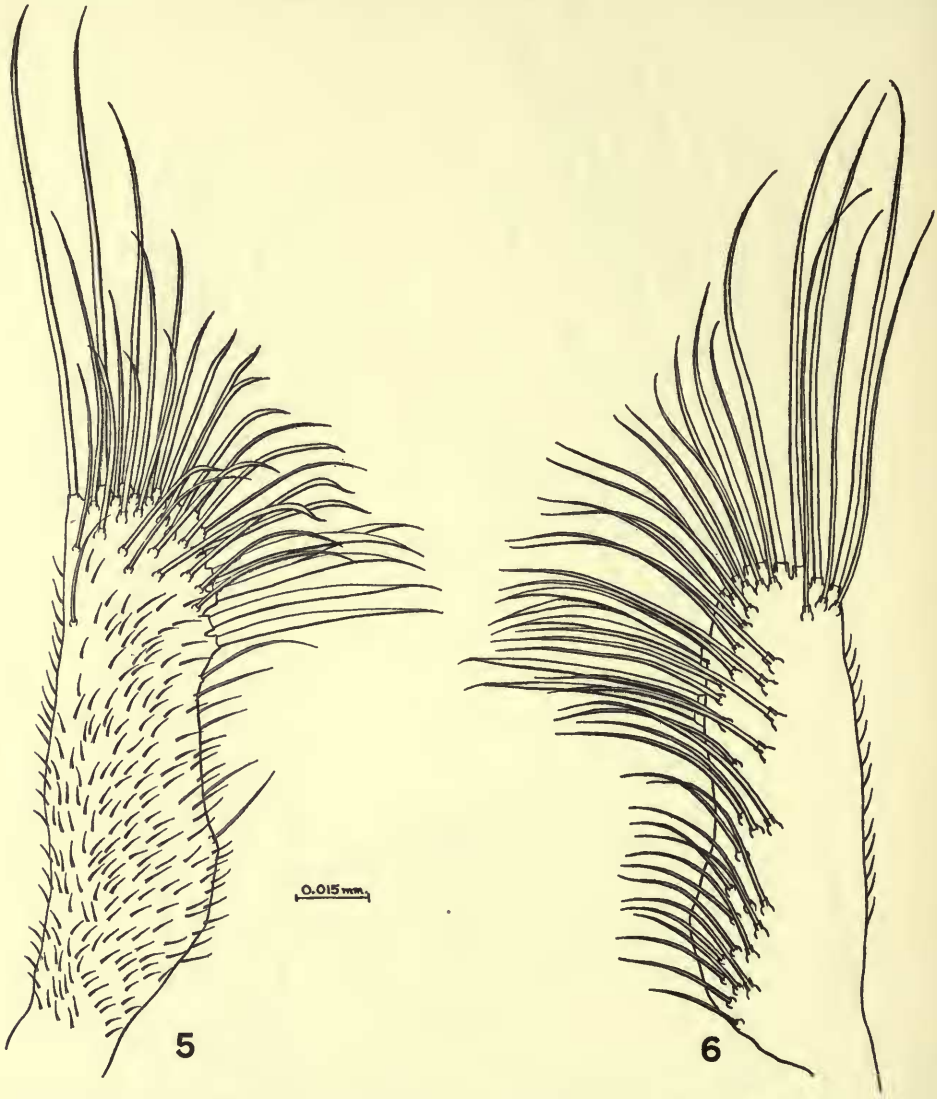
of genitalia which are conventionally drawn from the tergal aspect with the distal portions towards the top of the page. In this paper the view from the mid line of the genitalia is referred to as " inner lateral view " (illustrated in Fig. 2), and that of the side of the basal lobe nearest the coxite as " outer lateral view."

Certain of the setae of the basal lobe may be enlarged, thickened or flattened and arise from tubercles ; these are quite distinct in appearance from the remainder



FIGS. 3 and 4. Left basal lobe of ♂ coxite of *Aedes pseudoscutellaris* (Theobald). Fig. 3. Tergal view (B .7). Fig. 4. Sternal view (B. 7).

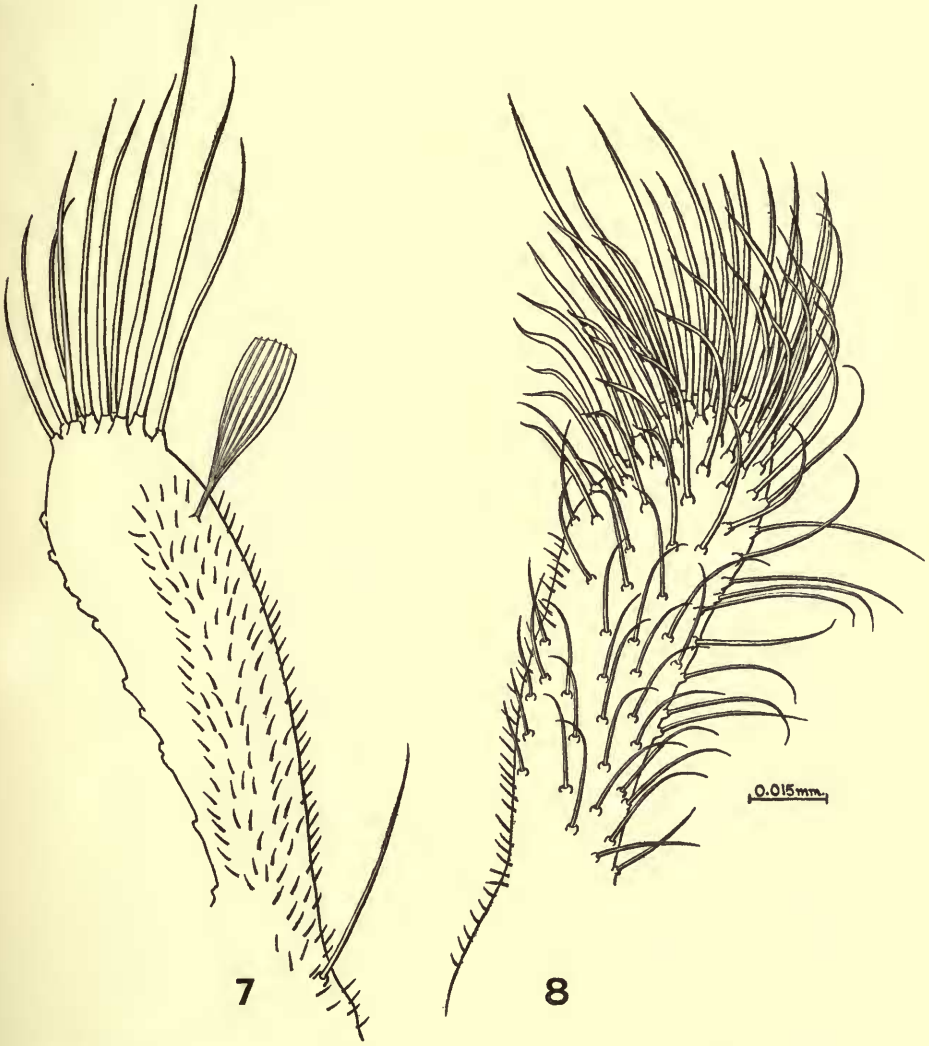
and are here referred to as specialized setae. Other authors have given them various designations (not always very clearly defined, but usually interpretable by reference to accompanying figures). The term does not include the very long hairs at the



FIGS. 5 and 6. Left basal lobe of ♂ coxite of *Aedes pseudoscutellaris* (Theobald). Fig. 5. Inner lateral view (B. 1). Fig. 6. Outer lateral view (B. 1).

tip of the lobe in some species which are thickened and elongated by reason of their size but do not differ in form from the majority—these are the "thickened bristles" of some authors. In several species a scale has occasionally been observed on the basal lobe (Fig. 7); it appears to be an aberration of no taxonomic significance.

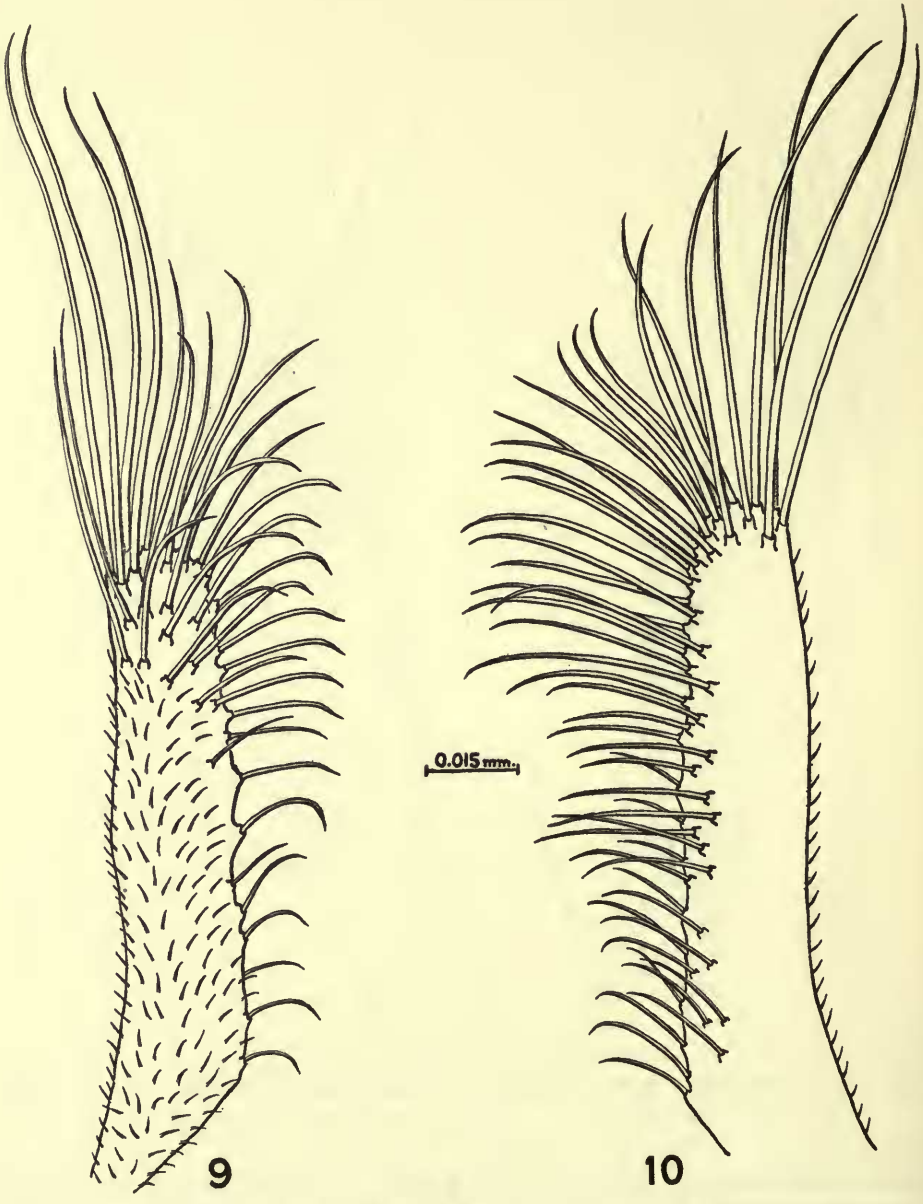
Edwards (1926) found differences in the length of the coxite compared with its breadth at the base; this ratio has not been recorded for most of the recently described species. Though the character by itself is not diagnostic it might be advantageous to have some note of it as it would give a basis of comparison where, as in many cases, the only part of the genitalia illustrated is the basal lobe.



FIGS. 7 and 8. Left basal lobe of ♂ coxite of *Aedes polynesiensis* Marks. Fig. 7. Tergal view (the scale is aberrant). Fig. 8. Sternal view. ♂, Taveuni, Fiji.

Edwards also observed differences in the style, whether slender or moderately stout, with tip swollen to varying degrees, and with its spine slender or stout, blunt or pointed. Such differences of degree are not very useful diagnostic characters, in

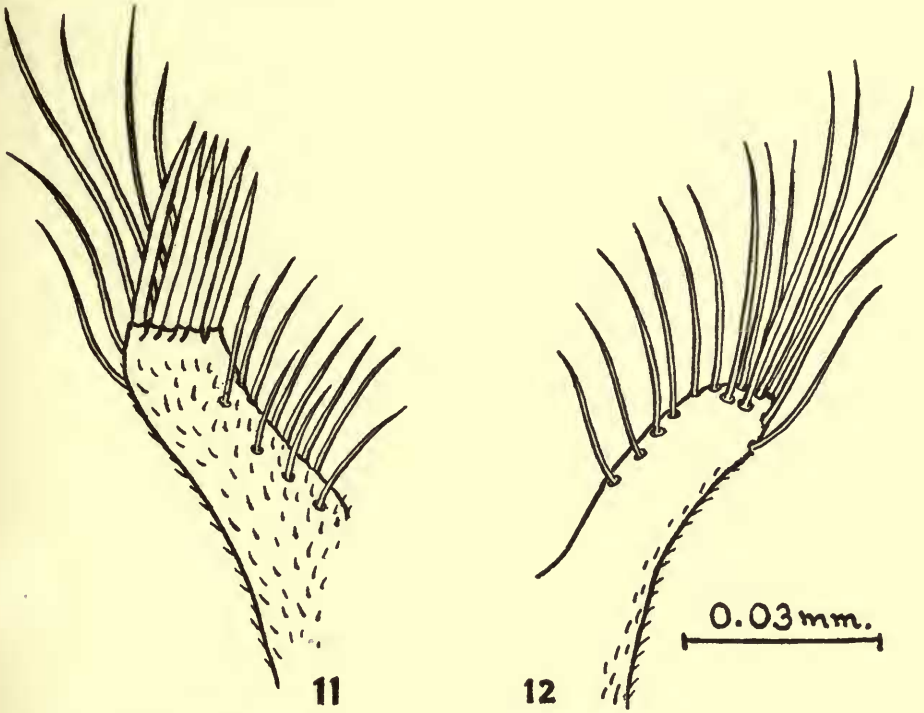
particular if other forms are not available for comparison. The appearance of the style depends to some extent on the way the specimen has been mounted. If the ratio of length of style to length of coxite were recorded, differences might be found between species. The spine varies even more with the mounting, as it is



FIGS. 9 and 10. Left basal lobe ♂ coxite of *Aedes polynesiensis* Marks. Fig. 9. Inner lateral view. Fig. 10. Outer lateral view. ♂, Suva, Fiji.

liable to shrink in diameter, and I have seen it appear quite different in two specimens of the one species.

Another character used by Edwards (1926) was the form of the ninth tergite—whether convex or emarginate—it is emarginate in *quasiscutellaris*, convex in most other species in which it has been described. The sclerotized portion of the tergite is narrow and very apt to become twisted in a mounted preparation, so that its shape is not always easy to interpret.



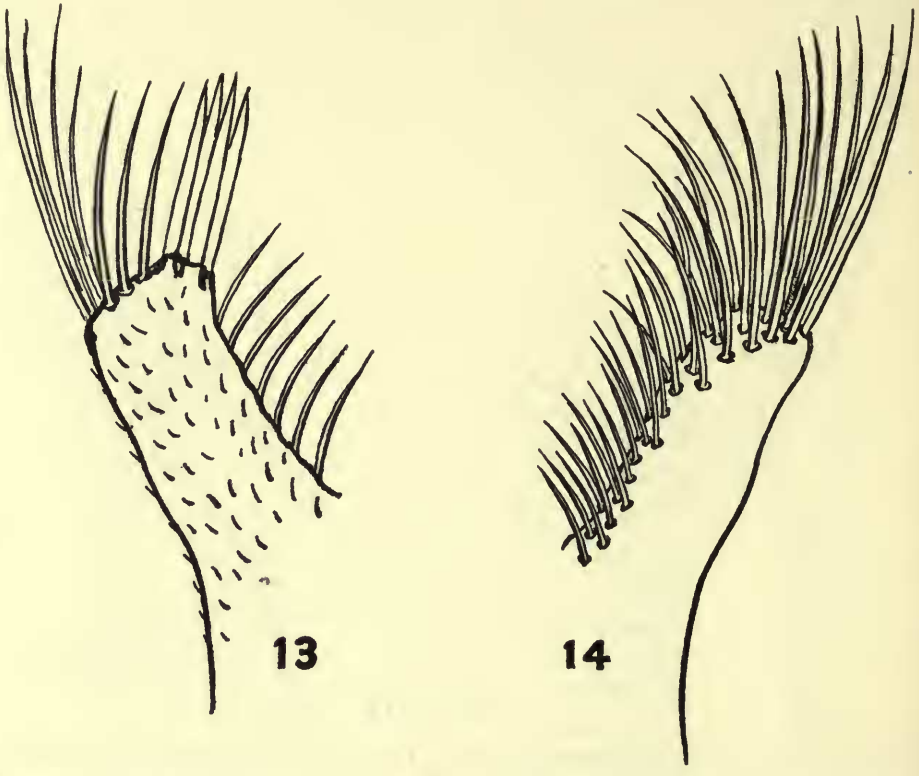
FIGS. 11, 12. Left basal lobe of ♂ coxite of sp. in *scutellaris* group from Andaman Is. Fig. 11. Inner lateral view. Fig. 12. Outer lateral view.

The character which Edwards observed as most important, the basal lobe, is now often the only part of the genitalia described or figured, since it has been found the most distinctive of all diagnostic characters used in separating the species of the *scutellaris* subgroup.

Edwards noted that the basal lobe differed in shape, the tip rounded, square-ended or conical; also in the length and disposition of the setae at the tip. He did not mention the occurrence on the basal lobe in any forms of stouter specialized setae, though his figure of *andrewsi* suggests they were observed in this species. The figures suggest (as do Edwards' preparation of genitalia of British Museum specimens) that the genitalia were mounted undissected; they were drawn in tergal view. He distinguished the basal lobe of *tongae* from that of "*pseudoscutellaris*" by the fact

that the former was hairy at the tip only and the latter hairy on the apical half or more. Edwards' figure shows the setae extending half-way down the tergal aspect of the basal lobe of "*pseudoscutellaris*," though in fact they occur on the sternal aspect. The specimen figured was from Samoa (= *polynesiensis*).

Barraud (1928) was the first to record the presence of specialized setae on the basal lobe. He observed in Andaman Is. form that a few of the setae at the apex of the



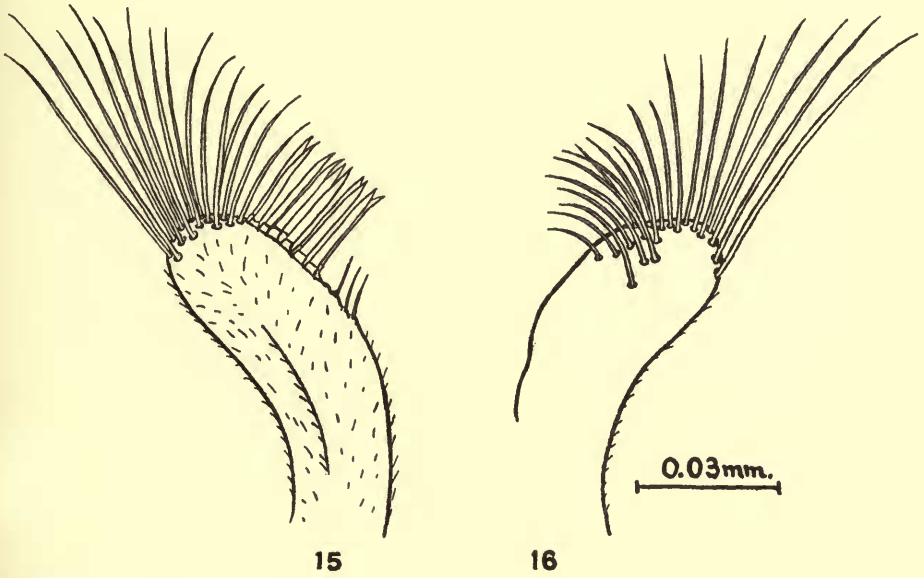
FIGS. 13, 14. Left basal lobe of ♂ coxite of *Aedes andrewsi* Edwards from Christmas I. Fig. 13. Inner lateral view. Fig. 14. Outer lateral view.

basal lobe are "stouter and more blade-like than the majority." Bonne-Wepster & Brug (1932) recognized the distinctive form of the basal lobe in *alorensis* and the presence of "a peculiar claspette-like, long and slender structure with two filaments at tip." (In my opinion really part of the basal lobe bearing specialized setae (see figure in Plate 18).

Farner & Bohart (1944) described and figured "enlarged bristles" (i.e., specialized setae) on the basal lobes of *pernotatus* and *scutellaris*. They made an important contribution to the methods of investigating the subgroup by the introduction of figures of the basal lobe in lateral as well as in tergal view. (They figured lateral

views for *scutellaris* and *guamensis*, but the latter from comparison with specimens is more a tergal than truly lateral view.) They also stated " the thickened bristles of the basal lobe in *guamensis* are less developed than those in *pseudoscutellaris*[1]." This might have been interpreted as a reference to specialized setae in which case the specimens of " *pseudoscutellaris* " would be true *pseudoscutellaris*. However, their illustration is of *polynesiensis* and Dr. Alan Stone (*in litt.*) informs me that the setae of the basal lobe in the latter are all slightly heavier than in *guamensis*.

Farner & Bohart (1945) referred to *quasiscutellaris* as having " a row of somewhat thickened bristles " and " no specialized setal group." They described the basal lobe of *tongae* as " without a specialized group of stout setae ; large bristles confined



FIGS. 15, 16. Left basal lobe of ♂ coxite of *Aedes tongae* Edwards from Sikiana, Solomon Is. Fig. 15. Inner lateral view. Fig. 16. Outer lateral view.

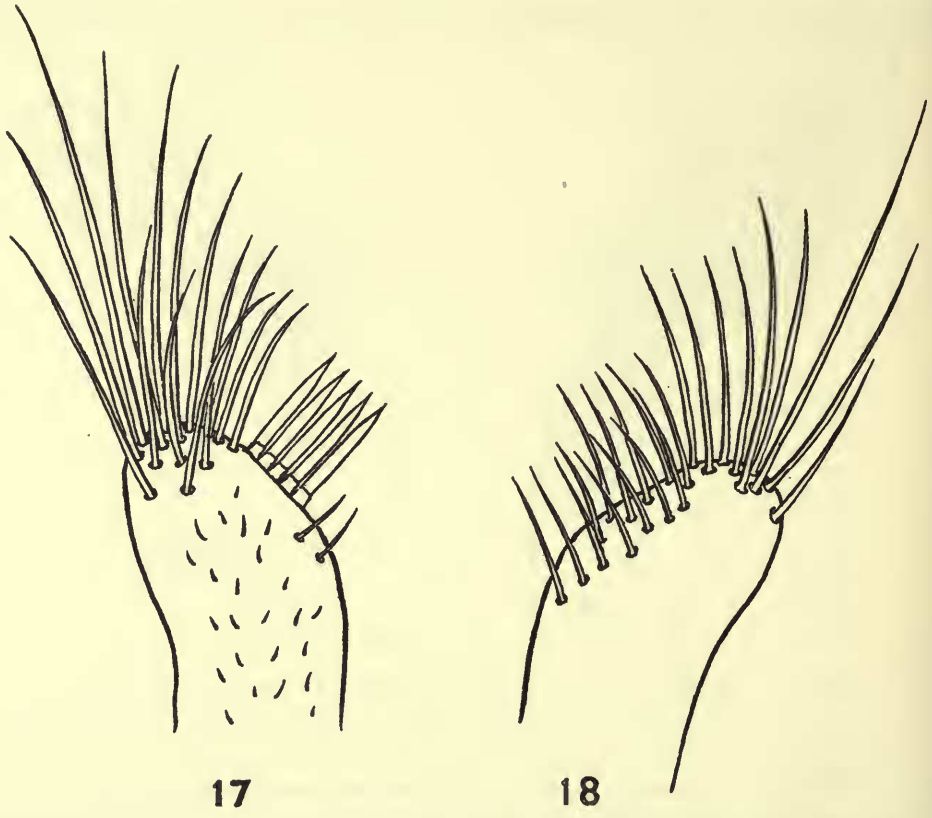
to apex, particularly in ventral view." They had seen one male from Vavau, Tonga Is., and figured the lobe in dorsal and ventral view. I have examined the basal lobe of a male of *tongae* from Sikiana, Solomon Is. in lateral view and it has 9–10 specialized setae (Fig. 15). It is not easy to judge with specimens mounted in tergal view but another Sikiana male appears to have 6 or 7. Three males from Tonga have 5 to 7 specialized setae which appear less strongly developed and more tapered than in those from Sikiana.

The same authors distinguished between " simple " (e. g., *tongae*) and " complex " (e.g., *quasiscutellaris*) basal lobes and noted whether the lobe is covered with minute setae tergally.

[1] Cf. Bohart & Ingram (1946*b*) who describe the basal lobe of " *pseudoscutellaris* " (= *polynesiensis*) as " largely covered with bristles, none of which appear as thickened setae."

Farner (1946) described the basal lobe of *hensilli* as similar to *guamensis* " but apparently with thickened bristles extending more basad." Bohart and Ingram (1946) distinguished two types of arrangement of specialized setae: " in a clump " in *scutellaris* as compared with " in a row " in *hensilli*.

The distinction is not a satisfactory one since an inner lateral view of the basal lobe of *s. scutellaris* shows the specialized setae in a row though in other views they often appear clumped. The basal lobe of *s. scutellaris* is square-ended in inner



FIGS. 17, 18. Left basal lobe of ♂ coxite of *Aedes guamensis* Farner & R. Bohart from Rota, Marianas. Fig. 17. Inner lateral view. Fig. 18. Outer lateral view.

lateral view and the specialized setae are grouped on the sternal angle of the tip (this occurs also in *andrewsi*) whereas in *hensilli* and species with similar basal lobes the tip is more rounded and the row of specialized setae extends down the sternal aspect of the lobe. Woodhill (1949*a*) described the genitalia of *s. katherinensis* as indistinguishable from those of *s. scutellaris*, " the basal lobe of the coxite carrying a series of hairs at the apex with several longer hairs joined to form a spine. The degree of development of this spine varies in both subspecies . . . ." I have examined

specimens of *s. katherinensis* from Woodhill's colony. The " spine " is the group of specialized setae which, as in *s. scutellaris*, often appear clumped, but in inner lateral view they are seen as a row of about six setae. From this aspect the lobe differs somewhat in shape from *s. scutellaris* ; the tip is more conical without a distinct angle sternally, and the row of specialized setae extends down the sternal aspect.

Knight and Hurlbut (1949) figured only the tergal view of the genitalia of *hakanssoni* and described it as " quite similar to *riversi* and *hensilli* " which presumably means that specialized setae are present though this is not indicated in figure or text. I have examined a paratype of this species, and, though difficult to make out, there do appear to be 3 or 4 broader setae in a row among the non-specialized ones.

It was the observation of constantly-occurring specialized setae on the basal lobe of the coxite of specimens from the laboratory colony at Cambridge which first drew attention to the distinctness of this form (*pseudoscutellaris*) from the widely distributed Polynesian form (*polynesiensis*) usually referred to when the name " *pseudoscutellaris* " was used.

There is usually one aspect of the basal lobe which shows the characteristic shape of the lobe, and the specialized setae to best advantage.

In species with complex basal lobes, which appear expanded in tergal view, such as *quasiscutellaris*, *pernotatus*, *horrescens* and *alorensis*, this aspect shows all that is needed for identification. In a species such as *paullusi* with a simple truncate lobe, the setae all visible tergally and none of them specialized, the same view is again sufficient. Most of the species with basal lobe simple or expanded in lateral view have only a few long setae at the tip visible tergally. Thus Fig. 1 which shows this aspect of *pseudoscutellaris* is an equally good illustration of *polynesiensis* and *tongae*, and shows nothing except in proportionate lengths of the parts of the genitalia, to distinguish it from Rotuma sp. and possibly also from *hensilli*, *hakanssoni*, *riversi*, *guamensis* and *andrewsi*. On these same basal lobes, the unspecialized setae may occur only towards the apex or may extend varying distances towards the base—if the latter they may do so on the sternal aspect of the lobe, as in *polynesiensis* (when they are adequately illustrated from an inner lateral or, if there are no specialized setae, a sternal view), or more towards the outer lateral aspect as in *pseudoscutellaris*.

Practice has varied in illustrating the lateral aspect of the basal lobe. Thus figures of the lateral view of *s. scutellaris* in Farner & Bohart (1944, 1945), Bohart & Ingram (1946*b*) and Knight & Hull (1952) and of *s. katherinensis* in Woodhill (1949*a*) all appear to be of the outer lateral aspect ; whereas those of *hensilli* and *riversi* in Bohart and Ingram (1946*b*) appear to be of the inner lateral aspect. Where specialized setae occur in a row, the illustration must show them in file to display their number and shape ; this, in all species examined, is best seen from the inner lateral view. I have drawn the outer lateral aspect for a number of species and find that it shows quite distinctive arrangements of the unspecialized setae which would be valuable adjuncts to the characters of the specialized setae. Figs. 3–18 demonstrate the necessity for dissection of the genitalia in forms with a simple basal lobe, and for illustrations of more than one aspect of it, in order to show all the distinctive features.

Where the basal lobe is simple it might be useful to record its length relative to the length of the coxite, taking them from a given level (e.g., the outer lateral angle at the base of the coxite). This ratio appears to differ between *pseudoscutellaris*, *polynesiensis* and *tongae* on the one hand and Rotuma sp. on the other, though one would need to see more than the single available specimen of the latter to be satisfied on this point.

A few authors have recorded the number of apical teeth on the phallosome but there is insufficient information to suggest whether there may be specific differences in this character.

(3) *Zoogeography*

Mosquitoes of the *scutellaris* subgroup are found in the eastern part of the Oriental region and in almost all parts of the Australasian region that lie within the tropics, though their distribution on the tropical portion of the Australian mainland is apparently rather limited. They range from the Andaman Is. in the west, north-east to Okinawa and south-east to Mangareva Is. and Pitcairn I., i.e., from approximately 93° E. to 130° W. and from 26° N. to 25° S.[1]

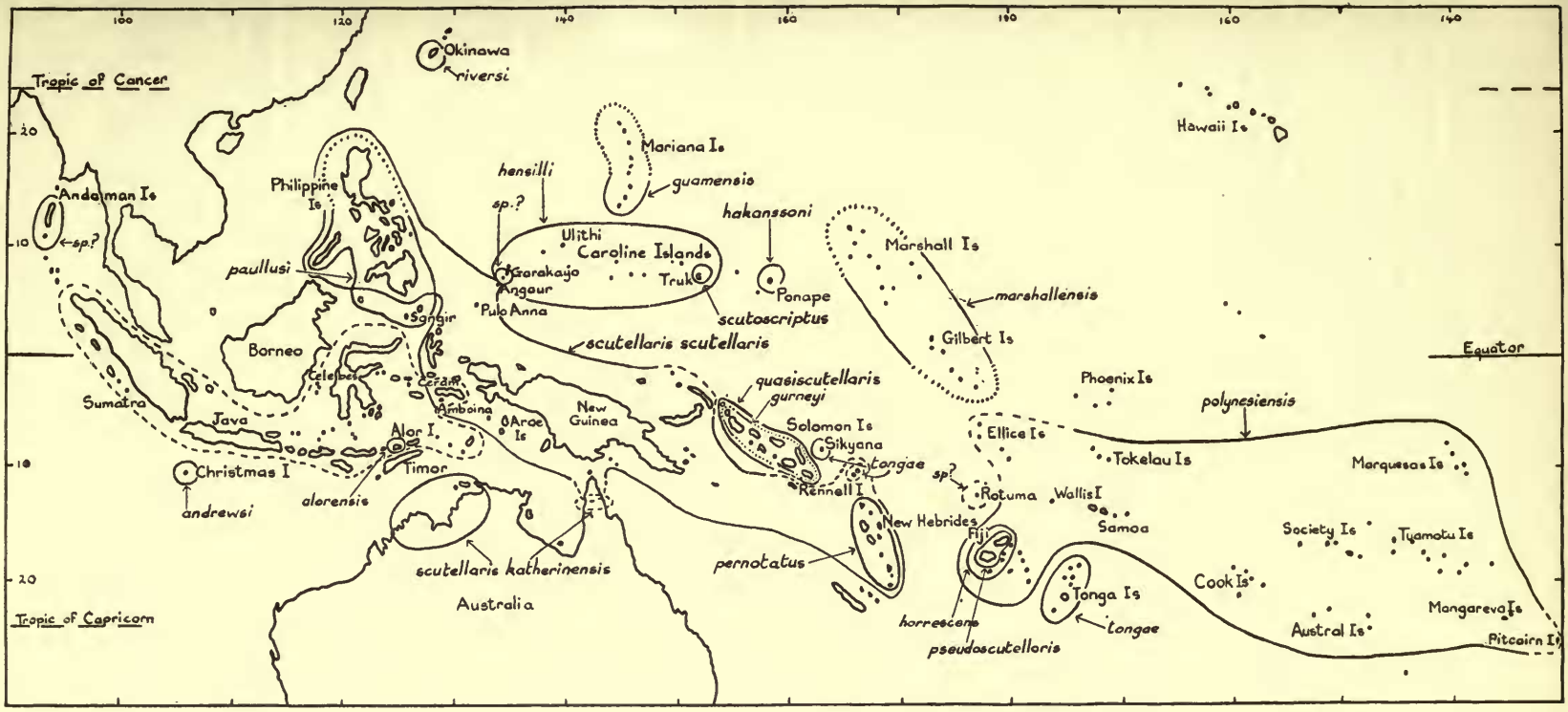
The present known distribution of the various members of the subgroup is shown in the accompanying map.[2]

In addition to well-established records, a distinction has been made on the map between definite records of the *scutellaris* subgroup, where it is the identity of the species that is in doubt, and comprehensive records which include a whole island group within the range of a species, though the localities given for it cover only a small portion of that range. Where the range of two species overlap, the known limits of the overlap are shown.

Most species of the *scutellaris* subgroup are confined to islands or groups of islands and are plainly examples of the process of speciation by geographical isolation. The origins of the insect faunas of Pacific islands have been discussed by, amongst others, Buxton (1935) and Zimmerman (1948). They are derived mainly from the west and are largely Indo-Malayan in origin. Farner & Bohart (1945) considered that superficially the *scutellaris* subgroup " appears to be of Polynesian or Melanesian origin, having spread westward into the insular parts of the Oriental region " but they acknowledged that with further knowledge of the subgroup, it might be necessary to modify or discard this suggestion. There seems no reason to suppose that members of this subgroup have spread naturally in a different direction from other mosquitoes and other insects. Moreover, they include the easternmost representatives of the subgenus *Stegomyia*, which extends throughout the Oriental and Ethiopian regions, and this in itself is strong evidence that the subgroup originated somewhere in the western part of its range, where also it overlaps the range of the closely allied *albopictus* subgroup.

[1] The specimen of *scutellaris* subgroup from Maldive Is., reported by Mattingly (see footnote, p. 353) extends the range westward to approximately 74° E.

[2] A copy of an earlier version of this map appears in Manson-Bahr & Muggleton (1952). The original contained no reference to *Anopheles punctulatus farauti*, and the indication in the published map, that its southern boundary of distribution is coincident with that of *s. scutellaris*, is incorrect except in New Hebrides.



GEOGRAPHICAL DISTRIBUTION OF THE *Aedes* (*Stegomyia*) *scutellaris* SUBGROUP.

———— Distribution of species definitely known.
. . . . . Distribution of species assumed continuous throughout island group.
– – – – *scutellaris* group recorded but identity of species not confirmed.

Though many of the species of the *scutellaris* subgroup are isolated from their fellows, there are several cases where the ranges of two or three overlap. If the distribution is treated in terms of island groups, the overlap appears considerable, but when details of locality records are examined, it is found that in some cases, as far as at present known, it is of small extent.

Apart from the records of recognized forms—Andamans sp., *andrewsi* from Christmas I., *alorensis* from Alor and *s. scutellaris* from Ceram, Aroe Is. amd Moluccas —there are numerous records of " *scutellaris* " from islands of the Malay Archipelago which have not been reassessed since the existence of many distinct species in the *scutellaris* subgroup was recognized. Brug (1932), Bonne-Wepster & Brug (1932, 1937) and Brug & Bonne-Wepster (1947) record mosquitoes of the *scutellaris* subgroup from Sumatra, Java, Lesser Paternoster Is., Celebes, Boeton, Kaboena, Adonare, Tenimber, Boeroe, Sanana, Saparoea and Sumba.

Brug & Bonne-Wepster (1947) also record *paullusi* from Celebes, Ceram, Amboina, Sanana and Sumatra. Since it has now been found that *alorensis* has an anterior white line on the mid femur, it seems possible that some of these records may refer to *alorensis*. For this reason, until further information is available, these localities have not been included in the range of *paullusi* on the map, but remain in the area of species of unconfirmed identity. *Paullusi* is known with certainty from Sangir and the southern half of Philippine Is.; in the latter it overlaps the range of *s. scutellaris* which occurs throughout the group. To the north the subgroup extends to Okinawa, where one species, *riversi*, is found.

The Caroline Islands stretch from east to west over 2,000 miles and five species[1] are known from them—*s. scutellaris*, *hensilli*, *scutoscriptus*, *hakanssoni* and sp. from Palau group. In the latter islands, at the western end of the chain, *s. scutellaris* is the only species recorded from Pulo Anna and Angaur; on Peleliu and Garakayo both *hensilli* and " sp. in *scutellaris* group " have been found. To the north-east *hensilli* is the only species known from Ulithi Atoll, and still further east it is found on five islands of Truk Atoll, on four of which *scutoscriptus* also occurs. At the eastern end of the Carolines chain, *hakanssoni* is the only species of the group found on Ponape. It is a reasonable supposition that *hensilli* was formerly confined to Ulithi and perhaps other islands as yet uncollected, and has subsequently extended its range both east and west to overlap in each direction that of another form. North of Caroline Is., a single species, *guamensis*, is known from Mariana Is., and to the east another, *marshallensis*, from Marshall and Gilbert Is.

The Philippines and Carolines records of *s. scutellaris* represent the north-west limits of its range. It extends south through New Guinea and I have seen specimens from Hammond Is., Torres Straits, within about 20 miles of Cape York. In the eastern islands of Torres Straits it occurs on Murray, Darnley, Nepean and Yorke Is. The subspecies *s. katherinensis* is known from Northern Territory and northern West Australia. The situation in north Queensland is interesting and requires elucidation. Mackerras (1946) mentioned the occurrence of *scutellaris* in unsettled parts of Cape York Peninsula adjacent to Thursday I.; his specimens have not been available for examination. Of two females from the Red Island Point area near

[1] Dr. R. M. Bohart has a sixth species, from Korror I. in the Palau group.

Cape York, one is apparently *s. scutellaris* with mid femora entirely dark anteriorly ; the other has three white scales scattered along the anterior surface of its remaining mid femur. Of five females from the Coen district, about 200 miles south of Cape York, two from Skull Creek are badly damaged ; the only remaining mid femur has three or four white scales scattered along its anterior surface. There are seven to fourteen white scales in this position in specimens from Coen and from Musgrave Station. The fifth specimen from Blue Mountains goldfield, has distinct but incomplete narrow lines of white scales on the anterior surface of its mid femora. In this it resembles one of Woodhill's *s. scutellaris* × *s. katherinensis* F^1 hybrids, rather than *s. katherinensis*. It must be remembered that *s. katherinensis* is known chiefly from specimens descended from one batch of eggs from Katherine, N.T., only six other specimens from two localities being recorded. It might be possible for the white line to vary to this extent in different stocks (cf., variation in white scaling on the proboscis of different stocks of *pseudoscutellaris* shown in Table V). On the other hand, Cape York Peninsula is the most likely place for a naturally interbreeding population of the two subspecies to occur. Whether or not this specimen is a hybrid, it indicates that *s. katherinensis* does occur on the Peninsula.

The north-east limits of *s. scutellaris* are Admiralty Is. and Bismarck Archipelago. As already noted, some Admiralty Is. specimens have atypical scutal or tarsal markings. Laird (1946) records *s. scutellaris* from New Britain, but Hill's (1925) record of "*variegatus*" from New Ireland has not been re-checked. Laird (1952) found *quasiscutellaris* on Nissan I., half-way between New Ireland and Solomons.

In the south-east *s. scutellaris* extends to New Hebrides where it occurs on numerous islands and overlaps the range of the local species, *pernotatus*. A possible physiological difference between *s. scutellaris* from New Guinea and New Hebrides is suggested by its incrimination as the vector of jungle dengue fever in New Guinea (Mackerras, 1946), whereas in New Hebrides Perry (1948) considered that it did not appear to be a vector of dengue in nature under normal conditions (though Daggy (1944) thought it a probable vector on epidemiological grounds). North of New Hebrides, Farner & Bohart (1945) quoted identifications of *s. scutellaris* from Rennell[1] and Bellona Is. in south-west Solomons, and of *s. scutellaris* and *tongae* from Nupani I. in Santa Cruz group. They considered these records needed confirmation by further collections.

The islands have been doubtfully included in the range of these species on the map.

In Solomon Is. both *quasiscutellaris* and the aberrant species, *gurneyi* are found ; the latter has been recorded only from Bougainville and Guadalcanal. *Tongae* has been collected on Sikiana an outlying island east of the Solomons, but is the only species known both from there and from Tonga.

In the eastern part of the subgroup's range there are several species, females of

[1] The identification of further specimens from these islands would be of particular interest. Professor G. D. Hale-Carpenter informs me (*in litt.*) that in its butterflies of the genus *Euploea*, Rennell differs considerably from other islands of the Solomons group, and it seems that it got some at least of its fauna directly from New Guinea's eastern tip via the Louisiade archipelago as stepping stones.

which are very difficult to distinguish from one another. *Pseudoscutellaris* and *polynesiensis* have until recently been treated together as "*pseudoscutellaris*"[1] and Rotuma sp. females[2] may be indistinguishable from *polynesiensis*, as also are some females of *horrescens*. It has been possible to check many of the records by examination of males and *polynesiensis* appears to be the only widely distributed species in this area. Specimens collected by Dr. Marshall Laird on Nukonono I. have confirmed that *polynesiensis* occurs in the Tokelau group. Until males have been seen, some doubt must be felt in particular about records from Ellice Is. and Wallis I., which are nearest to the ranges of other members of the subgroup.

Theobald's (1907) record of "*scutellaris*" from Pitcairn I. seems to have been overlooked by later authors. Though Theobald at that time included both *albopictus* and *scutellaris* in his concept of "*scutellaris*," it is very unlikely that this record referred to *albopictus* and highly probable that it was *polynesiensis*.

In Fiji three species occur; *polynesiensis* is here at the western limit of its range but *pseudoscutellaris* and *horrescens* are not known from elsewhere. Edwards (1935) suggested that *horrescens* might be the native Fiji form, and that "*pseudoscutellaris*" had been more recently introduced from Samoa. While it is likely that the wide-ranging *polynesiensis* is an introduction, not enough is known of the distribution of *pseudoscutellaris* to cast doubt on its endemicity. Though the most obvious explanation is that these sympatric species originally developed in geographical isolation, comparatively little is known of differences in their ecology which might affect speciation.[3] *Horrescens* does show differences in habits from "*pseudoscutellaris*," but now that the latter name is known to have covered two species, the subject needs re-examination.

The question arises why, when most of the species of the *scutellaris* subgroup have, as far as we know, a fairly restricted distribution, a few should have much more extensive ranges. The larval ecology of all is essentially similar, why should some species apparently be much more biologically aggressive than others?

A study of the literature suggests that there may be some correlation between a species' ability to extend its range and a combination of avidity for human blood and ability to colonize artificial containers. The only forms for which both latter characteristics are recorded are *s. scutellaris*, "*pseudoscutellaris*" (= *polynesiensis*), *hensilli*, *quasiscutellaris* and *riversi*. With the exception of the last two, each of these species overlaps in its range at least two other members of the subgroup. Table II gives a summary of the recorded habits of the species.[4]

The inference to be drawn is that the activities of man have had much to do with the spread of these species and also that almost certainly they originally developed

[1] Taylor's (1914) and Breinl's (1915) records of "*pseudoscutellaris*" from Papua can be assumed to refer to *s. scutellaris*.

[2] In one ♀ from Rotuma the ratio of the length of the white band on hind tarsal segment IV was 0·86; in one ♂, 0·79. This is longer than is usual in *pseudoscutellaris* and *polynesiensis*, and might prove a distinguishing character.

[3] Zimmerman (1948), as a result of his observations of insects on Pacific islands, considers that certain organisms appear to have selected certain environmental conditions. Rather than being what they are as the result of environmental influences, certain mutant forms seek out the niches best suited to them.

[4] Dr. R. M. Bohart informs me that Korror sp. breeds in pitcher plants and has a very distinctive larva.

in geographic isolation somewhere within their present range. Buxton and Hopkins (1927) have put forward a strong case for the distribution of "*pseudoscutellaris*" (= *polynesiensis*) through the islands of Polynesia by the agency of Polynesian canoes. They similarly explain the occurrence of *tongae* on Sikiana; little has been recorded of the habits of *tongae*. Marks (1950) found that a percentage of *pseudoscutellaris* eggs could survive up to three weeks immersion in sea water, suggesting the possibility of dispersal in small floating vessels, such as coconut husks; however, it is now doubtful whether *pseudoscutellaris* is widely distributed.

The fact that certain forms of the *scutellaris* subgroup are known from the same localities without apparent intergrades justifies their treatment by taxonomists as full species, but further investigation is needed of forms which replace one another geographically. Huxley (1940) has emphasized the necessity for detailed mapping of the boundaries and range changes of species and subspecies. Many more records are needed before this can be attempted for the *scutellaris* subgroup.

(4) *Plate and Key for Identification of Adults*

Plate 18 includes the twenty-one known forms in the *scutellaris* subgroup[1] and, as indicated, eighteen have been actually examined, though in two of these male genitalia were not seen. The data included are based on a study of all descriptions and figures available, supplemented by direct observations on specimens, and by notes on *gurneyi, marshallensis, scutoscriptus, hakanssoni* and sp. from Palau group, kindly made by Dr. Alan Stone from specimens in U.S. National Museum.

The previous discussion of the diagnostic characters of the *scutellaris* subgroup indicates the variability of these in some species. Each figure therefore represents what, as far as can be judged from the information available, would be the condition in an average specimen of that series.[2] In several cases where characters vary considerably and both extremes are well represented, this has been shown by duplication of the parts concerned; in the case of *pseudoscutellaris* some of the variation obtained experimentally has been indicated thus.

All drawings, except those of the basal lobe, are conventional. For example, no attempt has been made to indicate the distance of the white band from the base of the tergite. The lengths of the tarsal segments are in their correct proportions, but the width has been exaggerated. The width of the white bands on the tarsal segments is the outer (i.e., greatest) width; where the bands are interrupted by dark scales this is shown in the same figure though in the actual specimens the interruption (except in *andrewsi*) is on the inner side.

The descriptions from which the figures are drawn vary in detail. *Hensilli* and *s. katherinensis* are fully described. *Marshallensis* is described on the basis of

[1] Dr. R. M. Bohart has supplied the following details for Korror sp. of characters figured in Plate 1. *Proboscis*: no white scales on under side in female, a somewhat distinct line in male. *Scutum*: no white scales along anterolateral margin. *Scutellum*: silver scales on all lobes, black at apex of mid lobe. *Mid femur*: no anterior white line. *Hind femur*: anterior white marking sloping off ventrally, not tapering. *Hind tarsus*: white bands complete on II–V, covering $\frac{2}{5}$ III, $\frac{1}{2}$ IV, $\frac{3}{5}$ V. *Tergite V*: band usually, but not always, incomplete. *Basal lobe*: somewhat as in *riversi* but row of specialized setae in apical rather than subapical position.

[2] The faint line of yellowish brown scales under the proboscis of *scutoscriptus* has not been interpreted as a white streak.

TABLE II.—*Summary of Recorded Habits of Species of the* scutellaris *Subgroup**

Species	Bites man in nature	Breeding places. Coconut shells or husks	Breeding places. Artificial containers	Breeding places. Tree-holes	Miscellaneous	Disease carried
guamensis†	Rarely	+	+	+	Cut bamboos, taro leaf axil	..
gurneyi	..	..	..	+	Swamp pond, pandanus leaf	..
hakanssoni	No	+	+	+	Rain barrels	..
hensilli	Yes	+	+	+	Rock crevices, fallen coconut fronds; not leaf axils	..
horrescens‡	..	+ (rare)	+	+	Tin, bamboos, tree-ferns, barrels	..
marshallensis	Yes	+	..	+	Well, base of coconut fronds	..
paullusi	"Hovering about"	+	..	+	Rock pools, fallen coconut fronds, bamboos	..
pernotatus	No	+	+	+	Axil ot taro leaf	..
polynesiensis§	Yes	+	+	+	Crab holes, holes in cut bamboo; not leaf axils	Non-periodic filariasis, ? dengue.
quasiscutellaris	Yes	+	+	+	Leaf axils; holes in coral	Not dengue.
riversi	Yes	..	+	+	Small rock holes, cut bamboo	"Under suspicion."
scutellaris¶ *scutellaris*	Yes	+	+	+	Taro leaf axil, fallen coconut frond, split bamboo, puddle, well, canoe	Dengue (in New Guinea, apparently not in New Hebrides).
scutoscriptus	..	..	+	+	..	..
tongae	..	+	..	+	..	Assumed non-periodic filariasis.
Sp. from Palau	..	+	+	..	..	..

differences from *s. scutellaris* and *gurneyi* on the basis of differences from *albopictus*, but Dr. Stone has cleared up doubtful points for me. He has also provided a description of the characters illustrated for sp. from Palau group, of which only brief details were given by Bohart and Ingram (1946*b*). The illustration of the basal lobe of this species is copied from a sketch supplied by Dr. Stone ; he describes the lobe as follows : " The apex is somewhat angular, almost as in *marshallensis*, but lacking the two stout spines ; the hairs of the apex of the lobe (mediad) are thickened and curved and form a very distinct curved tuft." Bohart and Ingram's notes on the hind tarsus differ from Dr. Stone's, so both have been illustrated.

The differences in the figures of the basal lobe are probably in some cases more apparent than real and in others more real than apparent since they are from various sources. The drawing of the basal lobe of *scutoscriptus* is enlarged from a small figure of the complete genitalia and possibly suggests a closer resemblance to *pernotatus* and *alorensis* than actually exists. Dr. Stone informs me (*in litt.*) that an examination of the type slide of *riversi* shows the basal lobe to be more as in *s. katherinensis* than would appear from the figure in the chart.

Some species show the distinctive shape and specialized setae of the basal lobe best in tergal view. In others an inner lateral view is essential for correct interpretation. It is believed that the figures are drawn to meet these requirements. Unfortunately, sp. from Rotuma does not show the specialized setae in tergal view, and since a second male was not available from which a mount in lateral aspect could be made, the basal lobe is figured in sternal view ; this figure is therefore not directly comparable with any of the others.

It was thought proper to show a distinction between freehand and scale drawings. The former were made during visits to the British Museum (Natural History) and though they are believed to give an accurate representation, it was not possible to give the same time and care to details as in specimens which were examined in the laboratory in Cambridge or Brisbane ; the latter were drawn to scale.

The species are arranged in Plate 18 as far as possible in their geographical relation-

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* No information is available on the habits in nature of spp. from Andaman Is., or Rotuma I., nor of *andrewsi*, *alorensis*, *pseudoscutellaris* or *s. katherinensis* ; laboratory colonies of the last two feed readily on man. Bahr (1912) had both *polynesiensis* and *pseudoscutellaris* amongst the mosquitoes used when he proved " *pseudoscutellaris* " the vector of filariasis in Fiji (see Marks, 1951).

† Bohart & Ingram (1946*b*) report that adults of *guamensis* " are rarely seen in nature and have never been observed to bite man even in heavily breeding areas ". Reeves & Rudnick (1951) record 21 specimens of *guamensis* in a collection of 7767 mosquitoes taken biting man. Farner & Bohart (1945) quote Fullaway's report in 1912 of this species as " very abundant and troublesome in the forests " but it seems unlikely that this referred to *guamensis*. Laboratory experiments of Travis (1947) showed that *guamensis* would not feed readily on a dog but that in 68% of those which did, larvae of *Dirofilaria immitis* developed to the infective stage.

‡ Manson-Bahr & Muggleton (1952) found that adults of *horrescens* reared in the laboratory fed reluctantly on human blood and concluded from their experiments that this species was unlikely to be a suitable host for the local non-periodic filaria.

§ Buxton & Hopkins' (1927) records of breeding places of " *pseudoscutellaris* " refer to *polynesiensis*, the only species of the subgroup known from Samoa. Paine (1943) gives a long list of breeding places of " *pseudoscutellaris* " in Fiji but these may refer either to *pseudoscutellaris* or to *polynesiensis*. Perry (1950) quotes a personal communication from Lever reporting that " *pseudoscutellaris* " was an important agent in the transmission of dengue in Fiji—this might apply to either or both *pseudoscutellaris* or *polynesiensis*.

¶ Backhouse & Heydon (1950) found *scutellaris* inhospitable to *Wuchereria bancrofti* in the Rabaul region.

ships, so that those next to one on the plate are those nearest to it on the map. This was more difficult with species in the eastern part of the range of the group, and for interpretation of apparent trends in characters, the plate should be used in conjunction with the map.

It is hoped that the plate may overcome certain disadvantages of keys and tables. The visual presentation directs attention to resemblances and differences and the geographical arrangement brings out trends in characters and suggests relationships, some of them quite unexpected, which might otherwise escape notice. If an undescribed form were encountered, the plate should indicate the fact more strongly than a key can. Like keys and tables, however, the plate is not more than a preliminary guide and final identifications should always be made by reference to full published descriptions.

Though the plate was designed for use on its own, it might prove more useful in the field if a key were available or a preliminary guide. The following key has therefore been prepared. It gives a good indication of the necessity for examination of male genitalia for certain identification of a species. The plate obviates the need for a key to male genitalia.

Key to Adults of the *scutellaris* Subgroup

(Median white line on scutum relatively slender; hind tarsal segments I–IV basally banded, V basally banded or all white.)

1. Abdominal tergal markings basal; pleural markings in patches . *albopictus* subgroup.
   Abdominal tergal markings with more mesal portions basal; pleural markings in longitudinal bands; costa with white line on basal third . . . . *granti.*
   Abdominal tergal markings with more mesal portions sub-basal; costa all dark or with small basal white patch . . . . . *scutellaris* subgroup 2.
2. Pleural markings in patches . . . . . *gurneyi.*
   Pleural markings in longitudinal bands . . . . . 3.
3. Hind femur with white marking on anterior surface sloping off ventrally towards apex[1] 4.
   Hind femur with white marking on anterior surface tapering towards apex . . 7.
4. Abdominal tergites with triangular white lateral markings . . . . *guamensis.*
   Abdominal tergites with lunate white lateral markings . . . . . 5.
5. Scutellum with patches of dark scales on all lobes; hind tarsal V with apical half or more completely dark[2] . . . . . *hakanssoni.*
   Scutellum with small patch of dark scales at apex of mid lobe only; hind tarsal V white to apex on outer aspect . . . . . 6.
6. Scutum with wide white line along anterolateral margin; abdominal tergites with lateral patches only . . . . . *scutoscriptus.*
   Scutum dark on anterolateral margin; some abdominal tergites with complete bands . . . . . Palau sp.

[1] Since going to press I have seen four ♀♀ of *marshallensis* collected by Dr. M. Laird on Teaoraereke I., off Tarawa, Gilbert Is., in which the ventral dark scaling on hind femur is reduced; in two specimens the white marking on anterior surface still appears tapering, but in two it slopes off ventrally towards apex; the latter would key to the second half of couplet 5, being distinguished by the dark apical half of a hind tarsal V.

[2] Dr. R. M. Bohart has supplied the following note: Korror sp. keys out to couplet 5 but has hind tarsal V about ⅔ dark all around. Otherwise it agrees with the second half of the couplet and goes on to couplet 6 where it differs from either part by tergites sometimes having lateral patches only and scutum always dark on anterolateral margin.

7. Mid femur with longitudinal white line on anterior surface . . . . . 8.
   Mid femur dark on anterior surface . . . . . 10.
8. Scutum with narrow white line along anterolateral margin . . . . *paullusi*.
   Scutum dark on anterolateral margin . . . . . 9.
9. Proboscis with white streak ventrally. . . . . *alorensis*.[1]
   Proboscis dark ventrally . . . . . *scutellaris katherinensis*
10. Scutum with complete or incomplete narrow white or yellowish line along antero-lateral margin (at least, not less than five white scales) . . . . . 11.
    Scutum dark on anterolateral margin (at most, less than five white scales on scutal angle) . . . . . 12.
11. Some abdominal tergites with complete bands . . . . . *quasiscutellaris*.[2]
    Abdominal tergites never with complete bands . . . . *pseudoscutellaris*.
12. Hind tarsal V with black apex; some abdominal tergites with complete bands . 13.
    Hind tarsal V white to apex on outer aspect . . . . . 14.
13. Length of white band on hind tarsal IV, 0·2–0·4; on hind tarsal V, 0·2–0·5 length of segment . . . . . *marshallensis*.
    Length of white band on hind tarsal IV, 0·3–0·6; on hind tarsal V, 0·4–1·0 length of segment . . . . . *hensilli*.[3]
14. Some abdominal tergites with complete bands . . . . . 15.
    Abdominal tergites with incomplete dotted bands, or with lateral patches . . 16.
15. Proboscis with white streak ventrally. . . . . Andamans sp.
    Proboscis dark ventrally . . . . . *scutellaris scutellaris*.
16. Some abdominal tergites with almost complete dotted bands; proboscis with white streak ventrally . . . . . 17.[4]
    Abdominal tergites with lateral patches only . . . . . 18.
17. White scaling on one or more of hind tarsals III–V interrupted by dark scales on inner aspect . . . . . *tongae* (in part).
    White scaling on hind tarsals III–V not interrupted *riversi*, *horrescens*, *tongae* (in part).
18. Proboscis with white streak ventrally. . . . . *pernotatus*.[5]
    Proboscis dark ventrally . . . . . 19.
19. White band on hind tarsal IV interrupted by dark scales on outer aspect . *andrewsi*.
    White band on hind tarsal IV not interrupted . . . . . 20.
20. Length of white band on hind tarsal IV, not less than 0·8 length of segment Rotuma sp.
    Length of white band on hind tarsal IV usually less than 0·8 length of segment *polynesiensis*.[6]

(5) *Interspecific Relationships*

In considering the relationships of the species it can be seen from Plate 18 that different characters show trends in different directions. Where the affinities thus implied conflict with one another, it is impossible to say which is indicative of closer relationship. The tendency might be to regard the genitalia characters as of greatest importance. However, Woodhill (1950) has shown that differences in the basal lobe between *s. scutellaris* and *pseudoscutellaris* are not mechanical barriers to cross

[1] *Alorensis* is known only from one ♂; it is probable that *paullusi* ♀♀ with reduced anterolateral markings on scutum would be difficult to separate from *alorensis* ♀♀.

[2] Aberrant *s. scutellaris* from Admiralty Is. would key out here; *quasiscutellaris* with reduced line on scutum may key to *s. scutellaris*.

[3] Aberrant *s. scutellaris* from Admiralty Is. and New Hebrides would key out here; *hensilli* with hind tarsal V completely white will key to *s. scutellaris*.

[4] Some specimens of *s. scutellaris* have dotted bands and would key to couplet 16, but have no ventral white streak on proboscis.

[5] Some specimens of *horrescens* and *polynesiensis* may key out here; some specimens of *pernotatus* will key to *andrewsi* but the interruption to the hind tarsal bands is on the inner aspect.

[6] Some specimens of *horrescens*, *pernotatus* and *andrewsi* may key out here.

fertilization ; such differences therefore must be regarded from the same morphological standpoint as any other characters.

The *Aedes* (*Finlaya*) *kochi* group of mosquitoes has a similar distribution to that of the *scutellaris* subgroup though it does not extend quite so far into the Pacific. Marks (1947) observed that neither general coloration, nor structure of genitalia in the *kochi* group showed any obvious relationship to geographical distribution, but suggested that the affinities from New Guinea east might be traced in the larvae since the structure of the teeth of the lateral comb did appear to be related to geographical distribution. It would be exceedingly difficult to trace affinities in the larvae of the *scutellaris* subgroup, since many of them are so alike that they can only be identified doubtfully, if at all ; adult characters are a more promising field.

The white scaling on the proboscis is frequently a variable character and the trends it shows in distribution may be open to question. Species with a white stripe under the proboscis extend from Andaman Is. east to Alor (*alorensis*) and Philippines (*paullusi*) and north of the latter to Okinawa (*riversi*) ; there is a gap in distribution then as far as Solomon Is.[1] (*quasiscutellaris*), to the east of which the character appears in Sikyana and Tonga (*tongae*), New Hebrides (*pernotatus*) and Fiji (*horrescens* and sometimes *pseudoscutellaris*).

White scaling on the anterolateral margin of the scutum links *paullusi* in the Philippines east to the Caroline species *scutoscriptus* on Truk and *hakanssoni* on Ponape, south to aberrant *s. scutellaris* in Admiralty Is. and *quasiscutellaris* in Solomon Is., and east again to *pseudoscutellaris* in Fiji.

Since *hakanssoni* is the only species with distinctive scutellar scaling this character cannot be considered.

Species with a white anterior streak on the mid femur have a north-south distribution from Philippines to northern Australia, these are *paullusi*, *alorensis* and *s. katherinensis*. Dr. Alan Stone informs me (*in litt.*) that the mid femur of the type specimen of *riversi* " has a very narrow border of pale yellowish scales along the lower margin." Most species have pale scaling along the lower posterior margin of the mid femur and this sometimes extends on to the anterior margin. I have seen a specimen of *s. scutellaris* with a distinct white border along the lower anterior margin of the mid femur and probably the condition in *riversi* is comparable with this and not with the medially placed anterior streak of *paullusi*.

Four species are linked by having the white anterior scaling on the hind femur sloping off apically, instead of tapered as in the remaining seventeen forms. This character is found only in specimens from Marianas (*guamensis*) and Carolines (sp. from Palau, *scutoscriptus* from Truk and *hakanssoni* from Ponape).[2]

On the hind tarsi, the absence of a dark interruption to the band on segment I brings together species in the western part of the subgroup's range, Andamans sp., *alorensis*, *s. katherinensis* with *gurneyi* from Solomon Is. in the east, and sp. from Palau and *riversi* from Okinawa in the north.

There is a reduction in the width of the white hind tarsal bands linking species in

[1] The occurrence of related forms in Moluccas area and in Solomon Is. without intermediates in New Guinea is known in Lepidoptera (Zeuner, 1943) and Odonata (Lieftinck, 1949) and has been explained by Zeuner (*l.c.*) in terms of the theory of continental drift.

[2] Also in some specimens of *marshallensis* from Gilbert Is. (see p. 382).

a west-east line, *hensilli* in the western Carolines, *scutoscriptus* on Truk, *hakanssoni* on Ponape and *marshallensis* from Marshall and Gilbert Is.; these, except *scutoscriptus*, also have in common a black apical half to segment V (white in all other species and sometimes in *hensilli*).

Species which may have segments III–V or IV–V interrupted by a line of dark scales beneath, extend south-east from Marianas (*guamensis*) through Carolines (sp. from Palau, *scutoscriptus* from Truk, *hakanssoni* from Ponape) to Sikyana in Solomons, and Tonga (*tongae*); *pseudoscutellaris* in Fiji may show this character in certain environmental conditions, and it may occur in aberrant *pernotatus*. Far west of these species, *andrewsi* may have the band on segment IV interrupted, but dorsally, not ventrally.

Complete abdominal bands are found in species in the western and central part of the subgroup's range, from Andaman Is. sp., *alorensis* (Alor), *s. katherinensis* (N. Australia), *paullusi* (Philippines), *hensilli* and sp. from Palau (Carolines), *s. scutellaris* (New Guinea, etc.) to *quasiscutellaris* and *gurneyi* in Solomons, and north-east to *marshallensis* (Marshalls and Gilberts). On the outskirts of this distribution almost complete abdominal bands are found to the north, in *riversi* (Okinawa) and to the east in *tongae* (Sikiana and Tonga) and *horrescens* (Fiji).

The species which have only curving lateral patches on the abdominal tergites are found from Caroline Is. (*scutoscriptus*, *hakanssoni*) south-east to Rotuma sp. and *pseudoscutellaris* (Fiji) with *polynesiensis* ranging east from Fiji, and to the west, *pernotatus* in New Hebrides. North of Caroline Is., *guamensis* also has lateral patches but these are of distinctive shape. The exception to this distribution pattern is *andrewsi* from Christmas Is., far removed from the other species with lateral patches.

When one examines the form of the basal lobe, there is one particularly well-defined type, a simple lobe with a row of specialized setae along its sternal aspect. This can be traced from Okinawa (*riversi*) south-east through Marianas (*guamensis*), Caroline Is. (*hensilli* in the east, *hakanssoni* in the west) to Sikyana and Tonga (*tongae*) and Fiji (*pseudoscutellaris*). Rotuma sp. may be allied to this type and *polynesiensis* is essentially similar but has lost the specialized setae. Other species with a simple basal lobe are found in the western parts of the subgroup's range. The specialized setae are at the apex in Andaman Is. sp. and *andrewsi*, while *paullusi* has only non-specialized setae arising from its truncate apex. Though slightly expanded in lateral view the basal lobes of *s. scutellaris* and *s. katherinensis* are essentially similar to the simple type. There is a fairly close resemblance between *andrewsi* and *s. scutellaris*, both of which have the specialized setae set on the sternal angle of the tip; Dr. Stone has noted a resemblance between *riversi* and *s. katherinensis*.

Quite a different form of lobe is that with an elongated somewhat flattened apex, with specialized setae borne on its inner projection (i.e., towards midline of genitalia). This is found in the East Indian species *alorensis* (Alor) and in *pernotatus* (New Hebrides); *scutoscriptus* (Caroline Is.) appears to be similar; *quasiscutellaris* (Solomons) and *horrescens* (Fiji) though rather different, might be derived from this form; *gurneyi* which lacks specialized setae could be derived either from this, or

from further flattening of the apex of a lobe of *paullusi* type. *Marshallensis* has a similar inner projection, but the apex of the lobe is produced, not flattened, and it could derive almost equally well from the simple lobe first discussed ; sp. from Palau is apparently most like *marshallensis* but without specialized setae on the inner projection.

Although the distribution of the different characters may suggest different affinities, it is clear that (with one exception) there is a very definite west-east trend (as already pointed out, it is unlikely to be east-west), which is in accordance with known relationships of the fauna of Pacific islands. The notable exception is the north-south distribution of mid-femur pattern, but this is in the Indo-Australian portion of the range, where distribution of the fauna is a more complex problem.

(6) *Immature Stages*

Although, as already detailed, it was differences between larvae from different areas that first led to the recognition of the *scutellaris* subgroup, Farner & Bohart (1944) justly observed "An effective systematic revision of the larvae must await the availability of greater amounts of reared and associated material as well as a critical study of the taxonomic characters." No one has yet produced such a revision.

No details have been recorded of larvae of *andrewsi*, *alorensis*, *gurneyi*, *tongae* or spp. from Rotuma, Palau group and Andaman Is., though all except possibly *andrewsi*, *alorensis* and Rotuma sp. have been reared from larvae. Descriptions available for larvae of the other forms vary in their completeness from Woodhill's (1949*a*) note on the larvae of *s. katherinensis* " indistinguishable from those of *Aedes scutellaris scutellaris* " to Knight & Hurlbut's (1949) detailed account of the larva of *hakanssoni*.

Various authors have found characters for distinguishing the larvae where two species occur in the one locality. Edwards (1935) tabulated characters for separating larvae of *horrescens*[1] and " *pseudoscutellaris* " (Fiji) and indeed it was the observation of two distinct larval forms which led to the recognition of *horrescens* as a distinct species. Larvae of *pseudoscutellaris* and *polynesiensis* can be separated on the relative lengths of their gills (Marks, 1951*b*) so that the three Fijian species are identifiable. Perry (1944) gave key characters for distinguishing the larvae of *s. scutellaris* and *pernotatus* (New Hebrides). Bohart & Ingram (1946*b*) were able to distinguish *hensilli* larvae from those of *scutoscriptus* and sp. from Palau (Caroline Is.).

Belkin (1950) provided a system of nomenclature for the complete chaetotaxy of a culicine larva. With the aid of this and adequate representative larval material of the various species, it would very likely be found that many of the larvae could be identified on a combination of characters, as are the adults, and possibly some trends in the distribution of characters would appear. For example, examination of a small number of larvae of *pseudoscutellaris* and *polynesiensis* has suggested that hair 2 of abdominal segments III–VII is frequently single in *pseudoscutellaris* and

[1] Edwards gives a series of distinctive characters. The presence of multi-branched hairs on thorax and abdomen is not by itself sufficient to identify a specimen as *horrescens*, since occasionally these hairs are fairly heavily branched in larvae of *pseudoscutellaris* and *polynesiensis*.

rarely so in *polynesiensis*. Long series from varied localities are essential for evaluation of characters such as this. Our present knowledge is quite inadequate for preparation of a key to the larvae of the subgroup or for useful discussion of the specific larval characters.

No attempt has been made to separate species on pupal characters and the pupal stages have in general been ignored though Knight & Hurlbut (1949) give details of the pupa of *hakanssoni*, and Penn (1949) describes that of *s. scutellaris*.

The eggs of all species, so far as is known, appear identical but no comparative measurements for different species have been recorded.

III. EXPERIMENTAL STUDIES OF VARIATION IN *AEDES PSEUDOSCUTELLARIS* (THEOBALD)

(1) *Introductory*

The characters by which a culicidologist distinguishes the various members of the *scutellaris* subgroup from one another have already been discussed in detail.

Descriptions of some species indicated a certain amount of variation in several of the diagnostic characters. It was decided therefore to take a single species and investigate the extent to which such morphological characters of the adults could be affected by controlled variation of the larval environment. The results would give some indication of the reliability of the different characters for taxonomic purposes, and the factors involved in their phenotypic variation. They might thereby provide some evidence on the validity of the specific status accorded to the form investigated.

The common diagnostic characters of the subgroup were chosen for biometrical study. These all (except on the genitalia) concern the proportions of white scaling to black. Some additional characters of this type were studied, in view of their possible taxonomic use and also to discover whether they varied in a similar fashion to the rest. The measure usually given to indicate size of mosquitoes is the wing-length. This was recorded, and also for comparison, the length of the hind femur. It is a well-known zoological fact that size varies considerably with the temperature of the animal's environment, as well as from other causes such as, in mosquitoes, abundance of larval food.

In addition to these two measurements, the following characters were examined (each is discussed in further detail in conjunction with its appropriate table) :

White scales under the proboscis ; white scales on the anterolateral margin of the scutum ; white scales in front of the prescutellar bare area ; white patches at the bases of fore and mid tarsal segments ; extent of anterior white streak and of dark ventral scaling on hind femur ; greatest length of white bands on hind tarsi ; and least length (i.e., the extent to which they are interrupted beneath) ; distance between the lateral patches on abdominal tergites V and VI ; number of specialized setae on the basal lobe of the male coxite.

Variation was apparent also in several characters which were not investigated biometrically. In females bred at 15–16° C., the median white stripe on the scutum was the width of about five scales across, whereas at 30–32° C., it was 9 or 10 scales

across. At 30–32° C., broad appressed white scales were developed in certain sites where at lower temperatures the white scales were narrow curved.[1] This was particularly marked on the anterior margin of the scutum at the commencement of the median white stripe (some specimens from $\frac{1}{3}$ sea-water were similarly affected); a few broad scales were frequently present also at the posterior extremity of the median stripe, and on the scutal angle.

The studies of variation described herein were made on specimens derived from a laboratory colony, a small population which had been inbred for many generations. Though it seems probable that small populations are favourable to relatively rapid evolution (Mayr, 1942 ; Ford, 1949), they often show reduced variability due to accidental gene loss or genetically limited ancestry. It is therefore likely that the amount of variation observed in this stock is less than would occur in a natural population subject to the same conditions ; this is confirmed by a comparison with material from a colony of different origin. However, the specimens have been reared in controlled conditions, so that what variation does occur can be related to the variation in the environment.

Conditions were not controlled rigidly and the experiments were spread over a period of approximately sixteen months. It is therefore not surprising that when some of the series were tested for homogeneity in several cases appreciable heterogeneity was found. In this kind of exploratory work it is not necessary to make very precise measurements of the effect on each series of changing one factor in the environment and the interest is mainly in the qualitative differences. Nevertheless, comparison between Series F, C, B and E, in which the temperature was progressively raised while other conditions were the same, is very constant wherever any positive effect occurs at all.

The effects of the different treatments are illustrated in Tables III–XX. In certain cases where these were not clear-cut and it was a matter of interest to examine them further, their significance was tested statistically. In the tables, where specimens fall on the limits of two ratio groupings, they have in all cases been placed in the lower category.

(2) *Material*

The species chosen for investigation was *Aedes* (*Stegomyia*) *pseudoscutellaris* (Theobald) of which a culture was obtained from the following source :

The late Mr. D. W. Amos in August, 1948, sent by air larvae (all stages) of "*pseudoscutellaris*" from Fiji to Sir Philip Manson-Bahr in London. No particulars are now available of the number of specimens with which the colony was started, nor of the exact locality from which they had been collected, though it is believed to have been Suva. Mr. P. G. Shute established the laboratory colony and it was subsequently maintained as a continuously breeding population in the Parasitology Department of the London School of Hygiene and Tropical Medicine. From thence

[1] It would be interesting to know what factor is responsible for the development of a scale in one or other of two such distinct shapes. The distinction between narrow and broad scales on a given site is often used to separate species or even subgenera of mosquitoes.

a sample of all stages from egg to pupa was obtained in November, 1949. Approximately 350 adults were reared from it and their progeny are regarded as the first (Cambridge) generation. The studies of variation were made on specimens from this stock. Whether the original stock from Fiji was a pure culture of *pseudoscutellaris* is unknown, but there is no doubt that the sample brought to Cambridge was a pure culture of this species.

A second stock of *pseudoscutellaris* was received from Mr. B. A. O'Connor in April, 1951, direct from Fiji. This consisted of a batch of about 120 eggs obtained from wild-caught males and females, collected 10th–16th March at Naduruloulou Agricultural station (about 12 miles in a direct line east of north from Suva). Approximately 60 adults were obtained from this sample, and their progeny, reared under standard conditions, were compared with the other stock.

(3) *Methods*

(*a*) Rearing

The design of the experiments required that the conditions in which larvae were reared should be controlled, though highly refined techniques and rigorous control of all conditions were deemed unnecessary. A continuous breeding colony was not maintained; egg batches were hatched as required and the larvae reared with the following standard technique.

Breeding bowls were kept at the required temperature in thermostatically controlled incubators or in a constant temperature room. Straight sided glass bowls of varying capacity were used.

Larvae. The liquid contents of the bowl in which the eggs were to be submerged consisted of tap-water, " larval essence " and a small amount of larval food.

" Larval essence," used as a hatching stimulus,[1] was the filtered liquor in which a previous culture of larvae had been reared. It was stored in a jar and used as required in amounts of approximately 30–100 c.c. per bowl. The quantity was not standardized since there was no means of standardizing the quality.

The size of bowl and the volume of tap-water used were adjusted to the number of eggs to be hatched so that overcrowding of larvae was avoided.

Larval food consisted of a mixture of equal parts by volume of finely ground Bemax and two types of dog-biscuit, one of which contained meat-meal. It was fed either in aqueous suspension or the powder sprinkled directly on the surface of the medium. Larvae were fed as necessary, usually daily or every second day. Enough food was added to keep the liquid slightly cloudy, but to avoid formation of a scum. The medium soon developed a rich culture of micro-organisms and it is likely that these formed the bulk of the material actually ingested by the larvae.

Salinity. Specific gravity measurements made with an immersion hydrometer indicated no increase of salinity in tap-water culture media at completion of rearing at 25°–28° C., and in essence, when compared with tap-water at similar temperatures.

[1] Numerous workers have found that the presence of micro-organisms is one of the many factors that stimulate hatching in *Aedes* eggs, including Buxton and Hopkins (1927) in their studies of " *pseudoscutellaris* " (= *polynesiensis*). The effect of the " essence " may have been through the micro-organisms it introduced to the medium.

When rearings were made in diluted sea-water, the salinity was estimated by the method described by Harvey (1928) of titration with silver nitrate solution. The corrections he gives were applied and the results recorded in parts per thousand (‰) to the first decimal place. The salinity of selected samples from other conditions was measured in the same way.

Air. Compressed air was bubbled slowly through the larval medium; if this was not done a scum formed on the surface and larvae and pupae drowned.

Pupae were collected daily or every second day and transferred to a dish of clean water in a cage; in other respects the pupae were subjected to the same variations in environment as the corresponding larvae. When all pupae in the dish had emerged, the cage was transferred to a constant temperature room at 24–26° C.

Adults of all series were kept in cages (8 in. cubes or larger) in a constant temperature room at 24–26° C. The humidity of the room varied, but glass bowls with moist filter paper or porous earthenware pots of water were placed in the cages to provide moisture. Most specimens required for subsequent examination were killed 24–48 hours after emergence.

No food was given other than blood meals. The source of these was usually man, less frequently rabbit and once chicken. A blood meal was offered when the majority of females in the cage were 3–5 days old and continued long enough for numerous specimens to engorge (usually 20–30 minutes). Sometimes a second meal was given on a later day. Porous earthenware pots containing water were provided for oviposition. They were removed within 7 days of the blood meal and the water decanted, but the pots were kept moist for a further 1–2 days. They were stored in the constant temperature room at 24–26° C. and shards with the required quantity of eggs broken off when needed. Where egg batches were obtained from individual adults, these were laid on moist filter paper in a glass tube.

Specimens for study were usually pinned through the side as this was least likely to damage the characters studied. Each specimen received a label with its series letter (indicative of the conditions of rearing) and a serial number.

Records. Day by day records were kept for each batch of larvae reared. These included source and approximate or exact number of eggs; date submerged; particulars of medium; number of pupae collected; emergence of adults (in certain samples the proportions of the sexes were recorded from a count of pupal skins); date and source of blood meal; date of oviposition.

(*b*) Sampling

Sampling was at two levels, firstly from the total of adults reared in a batch, secondly from the collection of pinned specimens. In all cases damaged specimens were rejected. In the case of progeny of individual females, all suitable adults reared were pinned. With large collections of adults of mixed parentage, if none were needed for breeding, all were killed and the required number of specimens pinned. If it was desired to breed from the adults, each specimen for pinning was captured by hand in a glass tube. This method was found more satisfactory than an aspirator for the purpose of obtaining perfect specimens.

Pupation of a batch of larvae extended over a period of days. The pupae (and

adults emerged therefrom) in lots representing 1, 2 or 3 days pupation were kept in separate cages until samples had been taken. The majority of males emerged in the first few days, while the proportion of females gradually increased. The proportion of each sex to be pinned from any particular cage was in several cases known accurately from a count of sexes of the pupal skins. In most cases the numbers were estimated in the light of this experience, by direct observation of the adults to be sampled. The serial number of a pinned specimen indicated the batch from which it came and also the collection of pupae within that batch. The specimens examined represented proportionately the number pinned from each pupal collection within the batch. In this way a representative cross-section of the population was obtained.

It should be made clear, however, that though equal numbers of each sex from a batch might be pinned and equal numbers examined, the numbers of each sex actually reared in that batch were not necessarily equal.

From the males examined, a smaller number were selected on the same principle for dissection of the genitalia.

(*c*) Examination of specimens

The characters of the external morphology of the specimens were examined with a binocular dissecting microscope. Measurements were read on an eyepiece micrometer with divisions of 0·1 mm. ; using × 7 eyepieces and × 5 objective, 38 divisions of the scale represented 1 mm.

A rotating insect stage was used for orientating specimens for examination of characters.

Only one leg or wing (the one most easy to observe) was measured on each specimen.

Genitalia. The technique employed was a simple one which facilitated the preparation of a large number of mounts.

The specimen was relaxed and the terminal segments cut off and transferred to a small tube of 10% potassium hydroxide. This was set in a beaker of water, which was heated to boiling-point, and it was allowed to remain in the hot water for 5 minutes. The genitalia were transferred to a watch glass of distilled water, plus acetic acid. After five minutes they were transferred to cellosolve on an excavated slide and then dissected. With a straight surgical needle the genitalia were divided longitudinally into two halves, the basal lobe of one half was detached with the aid of fine steel pins.[1]

The parts were transferred to chloral gum medium on a slide, arranged so that both basal lobes were in lateral view, and covered with a piece of glass coverslip. They were examined with a monocular microscope using $\frac{1}{6}$ in. objective.

When required, scale drawings were made with the aid of a squared eyepiece micrometer.

[1] It is recommended that in specimens where the basal lobes are to be examined in lateral view, one lobe should be left attached to the coxite so that it may readily be determined which is the inner and which the outer lateral view.

(*d*) Variation of larval environment

Only one factor was varied in the larval environment in any one series of experiments.

An arbitrary " standard " series was reared as already described, in a tap-water medium at 25°–28° C. (Series B).

The following series were reared similarly but the temperature was varied :

15°–16° C. (Series F).
19°–22° C. (Series C).
30°–32° C. (Series E).

After preliminary experiments it was found that larvae could be reared satisfactorily in a medium containing $\frac{1}{3}$ sea-water. Series D was reared in $\frac{1}{3}$ sea-water at 25°–28° C.

Specimens of Naduruloulou stock (Series H) were reared similarly to Series B.

Attempts to rear larvae at 10° C., and at temperatures above 32° C. were unsuccessful.

The following summarizes the particulars for each series :

Series B. 25°–28° C.

About 40 batches representing nine generations were reared. Many of these were for the purpose of maintaining the stock, but 1,394 specimens (658 ♂♂, 736 ♀♀) were pinned from 19 batches, either mass rearings or individual egg batches. Specimens representing nine of these batches were studied ; they had been reared from December, 1949, to July, 1950. The 152 males examined came from six batches (1st generation mass rearing, 54 ; 3rd generation individual batches, 9, 9 ; 4th generation individual batches, 36, 14, 30). From the same batches respectively (excluding one 3rd generation batch) females were taken in the following numbers, 20, 10, 10, 10, 10 ; and in addition from a 3rd generation mass rearing (20) and 5th and 6th generation individual rearings (10, 10), making a total of 100, from eight batches. The mean temperature reading for the larval medium for one of these batches was 27·4° C. (6 readings). Genitalia of 25 males were dissected.

Series F. 15°–16° C.

One batch was reared in February-March, 1951, 350 specimens pinned (202 ♂♂, 148 ♀♀) and 100 of each sex examined. The batch was 9th generation (from Series C eggs, laid by females of 2nd generation bred at 19°–22° C.). Mean temperature was 15·2° C. (30 readings).

Genitalia of 25 males were dissected.

Series C. 19°–22° C.

Six batches were reared from February, 1950, to March, 1951, 500 specimens pinned (250 ♂♂, 250 ♀♀) and 100 of each sex examined. The first three batches (50, 50, 100 pinned adults) were from eggs from Series B (1st, 4th and 7th generations respectively). From the third of these, three succeeding generations at 19°–22° C

were bred (100 adults pinned from each). Twenty per cent of each lot of pinned specimens was examined, the sexes being equally divided.

The following are the mean temperatures of the medium for each batch, with the number of readings in parenthesis : 20·5 C. (8), 20·3 C. (9), 21·3° C. (3), 20·5° C. (19), 20·7° C. (19), 20·5° C. (10).

Gemitalia of 25 males were dissected.

Series E. 30°–32° C.

Four batches were reared from December, 1950, to March, 1951, 469 specimens pinned (lots of 60, 88, 300 and 21 totalling 260 ♂♂, 199 ♀♀), and 100 of each sex examined. From the above batches respectively were taken 35, 30, 21 and 14 males and 18, 28, 48 and 6 females. The first two batches were 8th generation eggs from Series B ; the third, 9th generation eggs from Series C (laid by female of 2nd generation bred at 19°–22° C.) ; the fourth, the progeny of the third. Mean temperatures of the medium for each batch (number of readings in parenthesis) were 31·1° C. (12), 30·7° C. (22), 30·6° C. (23), 29·9° C. (8).

Genitalia of 25 males were dissected.

Series D, 25°–28° C., $\frac{1}{3}$ sea-water.

Five batches were reared from June to November, 1950, in a medium of $\frac{1}{3}$ sea-water at 25°–28° C., 500 specimens pinned (250 ♂♂, 250 ♀♀) and 100 of each sex examined. The first batch was 6th generation eggs from Series B and the remainder were succeeding generations bred from these ; from each 100 adults were pinned, 20% of which were examined, the sexes being equally divided. For two batches the mean temperatures (number of readings in parenthesis) were 27·1° C. (4), 25·9° C. (9).

The following are the salinity measurements at the beginning and end of each rearing :

Initial salinity. (‰)	Number of days.	Final salinity. (‰)
11·7	23	16·2
11·9	15	13·1
12·1	13	12·7
11·9	13	—
11·7	15	15·0

The sea-water used was the laboratory stock from Lowestoft ; its salinity, measured on one occasion, was 34·6‰.

Genitalia of 25 males were dissected.

Series H. 25°–28° C.

One batch, the 2nd (Cambridge) generation of the Naduruloulou stock, was reared for study in April-May, 1951, 97 adults pinned (47 ♂♂, 50 ♀♀) and 25 of each sex examined. Two temperature readings of the medium were 27° C.

Genitalia of 10 males were dissected.

TABLE III.—*Aedes pseudoscutellaris*

Wing — *Length* (38 *units* = 1 *mm.*)

Males	Number of specimens	Length of wing*																		
		80–82	83–85	86–88	89–91	92–94	95–97	98–100	101–103	104–106	107–109	110–112	113–115	116–118	119–121	122–124	125–127	128–130	131–133	134–136
Series F, 15°–16° C.	100	—	—	—	—	—	—	2	3	22	52	19	2	—	—	—	—	—	—	—
Series C, 19°–22° C.	100	—	—	—	—	4	6	27	37	22	4	—	—	—	—	—	—	—	—	—
Series B, 25°–28° C.	150	—	—	1	15	36	40	8	—	—	—	—	—	—	—	—	—	—	—	—
Series E, 30°–32° C.	100	8	23	24	22	18	5	—	—	—	—	—	—	—	—	—	—	—	—	—
Series D, 25°–28° C., ⅓ sea-water	100	1	8	19	28	24	19	1	—	—	—	—	—	—	—	—	—	—	—	—
Series H, 25°–28° C., different stock	25	—	—	—	—	24	68	8	—	—	—	—	—	—	—	—	—	—	—	—
Females																				
Series F, 15°–16° C.	100	—	—	—	—	—	—	—	—	—	—	1	—	1	6	18	31	30	9	4
Series C, 19°–22° C.	100	—	—	—	—	—	—	—	—	—	—	—	2	7	17	33	22	14	5	—
Series B, 25°–28° C.	100	—	—	—	—	—	—	—	—	2	—	11	31	35	20	1	—	—	—	—
Series E, 30°–32° C.	100	—	—	—	—	4	16	19	28	26	4	3	—	—	—	—	—	—	—	—
Series D, 25°–28° C., ⅓ sea-water	100	—	—	—	—	—	—	—	8	20	18	30	18	5	1	—	—	—	—	—
Series H, 25°–28° C., different stock	25	—	—	—	—	—	—	—	—	—	4	32	56	8	—	—	—	—	—	—

* Numbers of specimens expressed in percentages.

(4) *Results*

(*a*) Tables III and IV : Length of wing and of hind femur

TABLE IV.—*Aedes pseudoscutellaris*

Hind femur *Length* (38 *units* = 1 *mm.*)

	Number of specimens	Length of femur.* 48–50	51–53	54–56	57–59	60–62	63–65	66–68	69–71	72–74	75–77	78–80	81–83	84–86	87–89
Males															
Series F. 15°–16° C.	100	—	—	—	—	—	1	21	56	20	2	—	—	—	—
Series C, 19°–22° C.	100	—	—	—	2	7	12	52	19	8	—	—	—	—	—
Series B, 25°–28° C.	152	—	—	—	2	24	49	25	—	—	—	—	—	—	—
Series E, 30°–32° C.	100	7	11	26	20	25	9	2	—	—	—	—	—	—	—
Series D, 25°–28° C., ⅓ seawater	100	—	—	2	22	49	21	6	—	—	—	—	—	—	—
Series H, 25°–28° C., different stock	25	—	—	—	—	12	48	40	—	—	—	—	—	—	—
Females															
Series F, 15°–16° C.	100	—	—	—	—	—	—	—	4	10	29	39	16	2	—
Series C, 19°–22° C.	100	—	—	—	—	—	—	—	2	13	23	38	21	1	2
Series B, 25°–28° C.	100	—	—	—	—	—	3	6	21	42	24	4	—	—	—
Series E, 30°–32° C.	100	2	3	5	12	32	25	16	5	—	—	—	—	—	—
Series D, 25°–28° C., ⅓ sea-water	100	—	—	—	—	7	12	37	29	14	1	—	—	—	—
Series H, 25°–28° C., different stock	25	—	—	—	—	—	—	—	16	76	8	—	—	—	—

* Numbers of specimens expressed in percentages.

The measurements have not been converted from the units in which they were made, since tabulation of these shows clearly the effects of different larval conditions.

Wing-length was measured from the large sclerite at the base[1] to the tip of the wing, excluding the fringe. The table shows that the longest wings are found in specimens bred at lowest temperatures, and conversely the shortest in those bred at the highest temperatures, with a gradient between. The wings of both males and females reared in ⅓ sea-water (Series D) are significantly shorter (at 0·1% level) than those reared in tap-water at the same temperature (Series B). Wings of females are longer than those of males in the same series.

The length of the hind femur was measured from its upper basal margin to the tip of the white patch at the apex. It shows a similar gradation to the wing-length in relation to temperature except that this is not apparent between females bred at 15°–16° C. and 19°–22° C. In Series D from ⅓ sea-water the femur is shorter

[1] At the wing base there is a complicated system of small sclerites ; the largest of these is a prominent dark shield-shaped sclerite lying just posterior to the base of the costa and articulating distally with the remigium (the united bases of veins of the radial complex). Prashad (1918) in his description of the wing-joint in Anophelines calls it the " epaulette " ; S. R. Christophers (personal communication) regards it as homologous with the 2nd axillary of Snodgrass (1935). It was found convenient to measure the wing-length from the proximal edge of the well-defined sclerite, rather than from the actual base of the costa which was not always easy to observe. The difference between measurements taken from these two points is less than 2% of the total wing-length and therefore of negligible importance in comparisons between species.

than in Series B from tap-water; the difference is highly significant. The femur is longer in females than in males from the same series.

The ratio of the length of the wing to that of the hind femur was plotted for several series. This showed some correlation but there was considerable scatter of the points, so that one could not be deduced from the other with any precision.

(*b*) Table V: Pale scales under the proboscis

TABLE V.—*Aedes pseudoscutellaris*

Proboscis		*Pale streak on under side*							
	Number of specimens	Number of pale scales*							
		0	1–10	11–20	21–30	31–40	41–50	51–60	61–70
Males									
Series F, 15°–16° C.	100	64	25	8	3	—	—	—	—
Series C, 19°–22° C.	100	32	52	13	3	—	—	—	—
Series B, 25°–28° C.	152	20	43	30	6	1	—	—	—
Series E, 30°–32° C.	100	16	48	20	13	3	—	—	—
Series D, 25°–28° C., ⅓ sea-water	100	17	69	13	1	—	—	—	—
Series H, 25°–28° C., different stock	25	—	8	12	16	36	12	8	8
Females									
Series F, 15°–16° C.	100	93	7	—	—	—	—	—	—
Series C, 19°–22° C.	100	67	28	5	—	—	—	—	—
Series B, 25°–28° C.	100	58	31	6	4	1	—	—	—
Series E, 30°–32° C.	100	64	31	5	—	—	—	—	—
Series D, 25°–28° C., ⅓ sea-water	100	66	31	3	—	—	—	—	—
Series H, 25°–28° C., different stock	25	—	—	24	12	24	20	16	4

* Numbers of specimens expressed in percentages.

The amount of pale scaling under the proboscis was recorded by an actual count of the number of pale scales. These observations led to the conclusion that a count of more than ten could be taken to represent the presence of a pale streak under the proboscis.

Ignoring for the moment the implications of the counts for Series H, the table illustrates that a pale streak is of much more frequent occurrence in males than in females. The variation of larval environment has had little effect on the amount of pale scaling in the female, except at the lowest temperature, 15°–16°, when a much higher proportion have the proboscis completely dark. This applies also to males at 15°–16° C., and there is a progressive reduction in the number of males with a recognizable streak at temperatures below 25°–28° C., but not an appreciable increase above. Series D in ⅓ sea-water also shows a reduction in numbers with a streak.

Series H, from different stock, has a very high proportion of both sexes with a streak. This emphasizes that though the observations of variation in one stock may suggest certain conclusions, it would be unsafe to interpret them as applying rigidly to all members of the species, let alone to related species.

(*c*) Table VI : Scutal pattern

TABLE VI.—*Aedes pseudoscutellaris*

Scutum	Number of specimens	*Extent of white scaling on anterolateral margin* Scutal pattern * (see Fig. 19).				
		B –	B	A –	A	A +
Males						
Series F, 15°–16° C.	100	65	30	4	1	—
Series C, 19°–22° C.	100	11	35	43	11	—
Series B, 25°–28° C.	151	—	4	14	82	—
Series E, 30°–32° C.	100	1	4	29	46	20
Series D, 25°–28° C., ½ sea-water	100	—	1	28	65	6
Series H, 25°–28° C., different stock	25	—	12	40	40	8
Females						
Series F, 15°–16° C.	100	69	29	2	—	—
Series C, 19°–22° C.	100	11	61	24	4	—
Series B, 25°–28° C.	100	5	16	59	20	—
Series E, 30°–32° C.	100	1	32	32	30	5
Series D, 25°–28° C., ½ sea-water	100	1	18	55	25	—
Series H, 25°–28° C., different stock	25	—	20	52	28	—

* Numbers of specimens expressed in percentages.

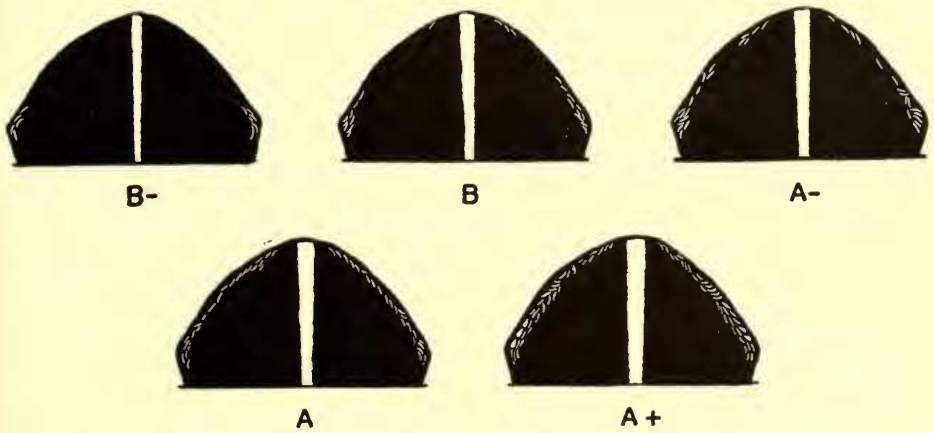

FIG. 19. Variation in white scaling on anterolateral margin of scutum of *Aedes pseudoscutellaris* (Theobald). (B –, F. 268 ; B, C. 44 ; A –, C. 152 ; A, D. 488 ; A +, E. 123 ; all ♀♀.)

The line of white scales along the anterolateral margin of the scutum distinguishes *pseudoscutellaris* from the closely similar species *polynesiensis*. The line may be definite, or faint and interrupted, but there are always some pale scales present.

For biometrical interpretation the amount of white scaling was divided into five categories, B –, B, A –, A, and A +, B – having the least and A + the greatest

development of white scales. These categories are illustrated from typical specimens in Fig. 19.

B— : white scales confined to a small patch on the scutal angle.

B : white scales on the scutal angle and extending forward slightly along the margin ; or else only on the scutal angle, with 2 or 3 scales further forward.

A— : white scales extending along the anterolateral margin, but the line interrupted to a greater or lesser extent, sometimes complete on one side and incomplete on the other.

A : white scales forming a narrow continuous line along the anterolateral margin.

A+ : white line on anterolateral margin quite thick and well marked.

There is no line of demarcation between these categories and interpretation is purely a matter of judgment, but by allotting the specimens among them, they do present a general picture of the variation in this character.

From the table it appears that at 15° C. the amount of white scaling is reduced to a minimum and the pattern is similar in both sexes ; with increase of temperature the white scaling increases, but to a greater extent in males than in females ; a larval environment of ⅓ sea-water does not appreciably affect it.

The presence of white scales on the anterolateral margin of the scutum is the only character known to distinguish females of *pseudoscutellaris* from *polynesiensis*. Specimens of the latter occasionally have 1–3 pale scales on the scutal angle. A count of the number of white scales on the scutal angle in specimens of *pseudoscutellaris* recorded as B— from all series, (165 out of a total of 1,101 examined) gave a range of 1–13 with a mean of approximately 6 scales for 299 scutal angles (one side of a specimen was sometimes rubbed or obscured).

(*d*) Table VII : White scales on either side of the prescutellar bare area

TABLE VII.—*Aedes pseudoscutellaris*

Scutum	Number of specimens	*White scales on either side of prescutellar bare area* Total number of white scales on both sides.*				
		0	1–4	5–8	9–12	13 or over
Males						
Series F, 15°–16° C.	100	31	54	14	1	—
Series C, 19°–22° C.	100	27	55	15	3	—
Series B, 25°–28° C.	135	6	61	27	6	—
Series E, 30°–32° C.	100	26	55	15	3	1
Series D, 25°–28° C., ⅓ sea-water	100	18	54	23	3	2
Series H, 25°–28° C., different stock	25	8	88	4	—	—
Females						
Series F, 15°–16° C.	100	50	39	10	1	—
Series C, 19°–22° C.	100	61	33	5	1	—
Series B, 25°–28° C.	100	41	42	13	3	1
Series E, 30°–32° C.	100	60	37	3	—	—
Series D, 25°–28° C., ⅓ sea-water	100	52	42	5	1	—
Series H, 25°–28° C., different stock	21	76	24	—	—	—

* Numbers of specimens expressed in percentages.

In certain species the white median line on the scutum divides into a definite fork on either side of the prescutellar bare area. In recording this character an actual count of the total number of white scales on both sides of the prescutellar bare area was made, and from these observations it was concluded that a count of more than eight represented a more or less complete fork.

The table shows comparatively little variation in this character and nothing that could be safely correlated with variation in larval environment. Only a very small percentage of specimens show a tendency to form a complete fork; males, however, do have a few more white scales than females.

The evidence suggests that this character is less subject to variation than some others concerned in scale pattern.

(*e*) Table VIII: White basal patches on fore and mid tarsi

TABLE VIII.—*Aedes pseudoscutellaris*

Fore and mid tarsi	Number of specimens	*White basal patches* *Some white scales at base of one or both segments*									
		Fore tarsus					Mid tarsus				
		I	II	III	IV	V	I	II	III	IV	V
Males											
Series F, 15°–16° C.	100	100	100	—	—	—	100	98	—	—	—
Series C, 19°–22° C.	100	100	100	1	—	—	100	99	—	—	—
Series B, 25°–28° C.	151	100	100	1	—	—	100	97	3	—	—
Series E, 30°–32° C.	100	100	100	1	—	—	100	100	1	—	—
Series D, 25°–28° C., ⅓ sea-water	100	100	100	1	—	—	100	99	—	—	—
Series H, 25°–28° C., different stock	25	100	100	—	—	—	100	100	—	—	—
Females											
Series F, 15°–16° C.	100	100	100	20	—	—	100	100	—	—	—
Series C, 19°–22° C.	100	100	100	12	—	—	100	100	—	—	—
Series B, 25°–28° C.	100	100	100	58	—	—	100	100	4	—	—
Series E, 30°–32° C.	100	100	100	92	1	23	100	100	21	—	—
Series D, 25°–28° C., ⅓ sea-water	100	100	100	66	3	13	100	100	11	—	—
Series H, 25°–28° C., different stock	25	100	100	72	4	8	100	100	16	—	—

* Numbers of specimens expressed in percentages.

One or more white scales at the base of a segment were interpreted as a white patch. Usually both tarsi of the pair were examined and a patch was recorded if there were white scales on one or both.

The table shows that *pseudoscutellaris* normally has white patches at the base of fore and mid tarsal segments I and II; the male seldom has more and in these characters is less subject to variation than is the female.

Females frequently have a white patch at the base of fore tarsal III and though there is no positive correlation with temperature at 15°–16° C. and 19°–22° C., there is a marked increase in the number with this character at 25°–28° C. and again at 30°–32° C.; larval environment of ⅓ sea-water does not produce any notable

effect. At 30°–32° C. and in ⅓ sea-water an occasional specimen has a patch on IV, and a higher proportion show one on V. The different stock of Series H show these characters at 25°–28° C. Below 25°–28° C. patches are absent from mid tarsal III; at this temperature few specimens show them, but there is a marked increase at 30°–32° C. and a lesser one in ⅓ sea-water; Series H again resembles the latter two series.

The more frequent occurrence of white patches on the fore tarsal segments than on the mid is rather unusual amongst mosquitoes and does not appear to have been observed in other members of the *scutellaris* subgroup. The usual tendency is for the amount of white scaling to be least on the fore tarsus, somewhat more extensive on the mid tarsus, and greatest on the hind tarsus.

(*f*) Tables IX and X: Extent of white anterior streak and ventral dark line on the hind femur

TABLE IX.—*Aedes pseudoscutellaris*

Hind femur	Number of specimens	*Length of anterior white streak* Ratio of length of streak to total length of femur.*				
		0·75–0·80	0·80–0·85	0·85–0·90	0–90–0·95	0–95–1·00
Males						
Series F, 15°–16° C.	100	—	32	67	1	—
Series C, 19°–22° C.	100	2	30	68	—	—
Series B, 25°–28° C.	152	—	16	84	—	—
Series E, 30°–32° C.	100	—	29	70	1	—
Series D, 25°–28° C., ⅓ sea-water	100	—	12	84	3	1
Series H, 25°–28° C., different stock	25	—	44	56	—	—
Females						
Series F, 15°–16° C.	100	—	58	42	—	—
Series C, 19°–22° C.	100	1	37	62	—	—
Series B, 25°–28° C.	100	—	49	51	—	—
Series E, 30°–32° C.	100	2	44	54	—	—
Series D, 25°–28° C., ⅓ sea-water	100	1	30	69	—	—
Series H, 25°–28° C., different stock	25	—	44	56	—	—

* Numbers of specimens expressed in percentages.

The hind femur at its base joins the trochanter, which projects ventrally a short distance taken from the base of the femur. All measurements taken from the base of the femur were taken towards the dorsal side; if taken from beneath they would have been slightly shorter.

The length of the white anterior streak has not been used taxonomically, nor is it likely to be of value in that respect since many species have it apparently equally developed. However, the opportunity was taken to investigate whether this character varies in the same way as other characters of white scaling. Table IX shows no apparent correlation between the length of the streak and the conditions in which larvae of the different series were reared.

TABLE X.—*Aedes pseudoscutellaris*

Hind femur	Number of specimens	*Distance from base of femur to beginning of dark ventral scaling* Ratio of distance to total length of femur.*				
		0	0·01–0·10	0·10–0·20	0·20–0·30	0·30–0·40
Males						
Series F, 15°–16° C.	100	18	—	44	34	4
Series C, 19°–22° C.	100	25	2	48	25	—
Series B, 25°–28° C.	152	12	1	18	48	21
Series E, 30°–32° C.	100	3	—	14	65	18
Series D, 25°–28° C., ⅓ sea-water	99	13	1	19	59	8
Series H, 25–°28°c., different stock	25	4	—	8	76	12
Females						
Series F, 15°–16° C.	100	34	3	39	22	2
Series C, 19°–22° C.	100	31	2	32	35	—
Series B, 25°–28° C.	100	19	4	28	43	6
Series E, 30°–32° C.	100	7	—	25	56	12
Series D, 25°–28° C., ⅓ sea-water	100	6	1	29	55	9
Series H, 25°–28° C., different stock	25	—	—	12	72	16

* Numbers of specimens expressed in percentages.

A possible difference was observed between *pseudoscutellaris* and *polynesiensis* in the extent of the dark ventral scaling on the hind femur. The amount of variation in this character in *pseudoscutellaris* was therefore investigated. The measurement was made from the base of the femur, as above, to the beginning of the dark scaling. If a line of dark scales reached right to the base ventrally, it was counted as zero, though owing to the trochantal projection, the micrometer reading was a small number. This explains the low frequency in the 0·01–0·10 ratio in Table X, as compared with that in Groups 0 and 0·10–0·20. This fault was not serious from a point of view of comparison with other species. Table X shows that this character follows the general trends already shown for others. The amount of dark scaling is greatest at low temperatures and following a gradient, becomes least at 30°–32° (though this gradation is not found between males at 15° C. and 19°–22° C.) ; ⅓ sea-water apparently does not affect it.

It may be added here that of 33 specimens of *polynesiensis* from various localities examined for this character 3 fell in the category 0·20–0·30, 9 in 0·30–0·40, 20 in 0·40–0·50, and 1 in 0·50–0·60. This suggests a difference between the two species, but it may be a geographically variable character ; insufficient specimens of *polynesiensis* from Fiji were examined to indicate whether it would be a useful character there.

(*g*) Tables XI–XVIII : The bands on the hind tarsal segments

Each band was measured at its greatest length, i.e., from the base to the further

extremity of the white scales ; the bands were longest on the upper anterior (outer) surface of the segments.

The band on hind tarsal segment I was always interrupted by a dark line beneath. The bands on II–IV were measured also at their least length, i.e., from the base of the segment to the nearest dark scaling which was continuous to the apex. Sometimes a band was slightly interrupted by dark scales at its base but formed a continuous ring distal to these ; such interruptions were ignored. In other words, the measurements of least length are of the difference between the greatest extent of continuous dark scaling and the total length of the segment. Bands were narrowest on the lower posterior (inner) surface of the segment.

A continuous line of dark scales beneath, even if only one scale in width was regarded as a complete interruption ; sometimes these scales were greyish rather than black, but contrasted with the white.

Table XI : White band on hind tarsal segment I

TABLE XI.—*Aedes pseudoscutellaris*

Hind tarsal, Segment I		*Greatest length of white band* Ratio of white band to total length of segment.*				
	Number of specimens	0·15–0·20	0·20–0·25	0·25–0·30	0·30–0·35	0·35–0·40
Males						
Series F, 15°–16° C.	100	7	82	11	—	—
Series C, 19°–22° C.	100	3	72	25	—	—
Series B, 25°–28° C.	151	—	13	85	2	—
Series E, 30°–32° C.	100	—	3	71	25	1
Series D, 25°–28° C., ⅓ sea-water	100	—	15	75	10	—
Series H, 25°–28° C., different stock	25	—	—	72	28	—
Females						
Series F, 15°–16° C.	100	3	82	14	1	—
Series C, 19°–22° C.	100	—	73	27	—	—
Series B, 25°–28° C.	100	—	11	79	10	—
Series E, 30°–32° C.	100	—	1	57	39	3
Series D, 25°–28° C., ⅓ sea-water	100	—	6	80	14	—
Series H, 25°–28° C., different stock	25	—	—	84	16	—

* Numbers of specimens expressed in percentages.

The length of the band varies in relation to the temperature gradient, being least at 15°–16° C., and greatest at 30°–32° C. It is apparently not affected by a larval environment of ⅓ sea-water. Females from the different stock, Series H, do not differ from others reared at 25°–28° C., but the males resemble those reared at 30°–32° C. The length of the band varies little between males and females of the same series.

Tables XII and XIII : White band on hind tarsal segment II

TABLE XII.—*Aedes pseudoscutellaris*

Hind tarsal, Segment II	Number of specimens	*Greatest length of white band* Ratio of white band to total length of segment.* 0·20–0·25	0·25–0·30	0·30–0·35	0·35–0·40	0·40–0·45
Males						
Series F, 15°–16° C.	100	4	81	15	—	—
Series C, 19°–22° C.	100	4	60	34	2	—
Series B, 25°–28° C.	152	1	15	62	22	—
Series E, 30°–32° C.	100	—	5	53	40	2
Series D, 25°–28° C., ⅓ sea-water	100	—	8	66	26	—
Series H, 25°–28° C., different stock	25	—	—	72	28	—
Females						
Series F 15°–16°c.	100	2	82	15	1	—
Series C, 19°–22° C.	100	3	50	46	1	—
Series B, 25°–28° C.	100	—	9	60	31	—
Series E 30°–32° C.	100	—	—	23	71	6
Series D, 25°–28° C., ⅓ sea-water	100	—	1	47	51	1
Series H, 25°–28° C., different stock	25	—	4	68	28	—

* Numbers of specimens expressed in percentages.

TABLE XIII.—*Aedes pseudoscutellaris*

Hind tarsal, Segment II	Number of specimens	*Least length of white band* Ratio of white band to total length of segment* 0	0·01–0·05	0·05–0·10	0·10–0·15	0·15–0·20	0·20–0·25	0·25–0·30
Males								
Series F, 15°–16° C.	100	76	1	10	13	—	—	—
Series C, 19°–22° C.	100	30	1	5	28	34	2	—
Series B, 25°–28° C.	150	1	—	1	9	49	35	5
Series E, 30°–32° C.	100	2	—	—	2	41	46	9
Series D, 25°–28° C., ⅓ sea-water	100	2	—	—	10	52	34	2
Series H, 25°–28° C., different stock	25	—	—	—	—	44	56	—
Females								
Series F, 15°–16° C.	100	78	4	2	12	4	—	—
Series C, 19°–22° C.	100	20	1	3	31	40	5	—
Series B, 25°–28° C.	100	—	—	—	5	41	49	5
Series E, 30°–32° C.	100	—	—	—	1	20	53	26
Series D, 25°–28° C., ⅓ sea-water	100	—	—	—	—	35	57	8
Series H, 25°–28° C., different stock	25	—	—	—	—	36	64	—

* Numbers of specimens expressed in percentages.

The band, both in its greatest and in its least length, follows the temperature gradient; the amount of white scaling increases from 15°–16° C. up to 30°–32° C.

Considering the greatest length of the band, males appear unaffected by ⅓ sea-water but females show a slight increase in white scaling.

Females reared at 30°–32° C. and in ⅓ sea-water in both measurements show more white scaling than males of the same series.[1]

In regard to the least length of the band the most noteworthy effect of the varied conditions is the appearance at low temperatures of a high proportion of specimens with the band completely interrupted by dark scales. Females from ⅓ sea-water show a slight increase in the white scaling but males are not affected. The different stock of Series H also has slightly more white scaling.

Tables XIV and XV : White band on hind tarsal segment III

TABLE XIV.—*Aedes pseudoscutellaris*

Hind tarsal, Segment III		*Greatest length of white band* Ratio of white band to total length of segment*							
	Number of specimens	0·30–0·35	0·35–0·40	0·40–0·45	0·45–0·50	0·50–0·55	0·55–0·60	0·60–0·65	0·65–0·70
Males									
Series F, 15°–16° C.	100	2	55	36	7	—	—	—	—
Series C, 19°–22° C.	100	—	13	61	26	—	—	—	—
Series B, 25°–28° C.	152	—	2	43	49	5	1	—	—
Series E, 30°–32° C.	100	—	—	8	50	30	12	—	—
Series D, 25°–28° C., ⅓ sea-water	100	—	—	19	64	13	4	—	—
Series H, 25°–28° C., different stock	25	—	—	16	68	16	—	—	—
Females									
Series F, 15°–16° C.	100	1	46	49	4	—	—	—	—
Series C, 19°–22° C.	100	—	6	48	46	—	—	—	—
Series B, 25°–28° C.	100	—	—	5	72	19	4	—	—
Series E, 30°–32° C.	100	—	—	1	23	39	30	6	1
Series D, 25°–28° C., ⅓ sea-water	100	—	—	2	39	30	18	2	—
Series H, 25°–28° C., different stock	25	—	—	4	72	20	4	—	—

* Numbers of specimens expressed in percentages.

The bands show the same correlation with temperature as do those on Segments I and II. Both males and females from ⅓ sea-water show an increase in the greatest length of the band ; the females do so in the least length also but it is not affected in the males. Males of different stock (Series H) have slightly longer bands, but not the females ; neither differ much in the least length from the original stock. In all series the females have slightly longer bands than the males and less extensive dark scaling beneath. At 15°–16° C. a high proportion of both sexes have the white band completely interrupted.

[1] This effect is no doubt partly due to the fact that, as many females emerge later than the males, their immature stages have had longer in the abnormal conditions. It was observed that in a proportion of specimens from these two series the tarsal segments did not become fully extended after emergence ; grossly abnormal specimens were not used for measurements, but in others this had probably occurred to a less marked degree.

TABLE XV.—*Aedes pseudoscutellaris*

Hind tarsal, Segment III — *Least length of white band*

Ratio of white band to total length of segment*

	Number of specimens	0	0·01–0·10	0·10–0·20	0·20–0·30	0·30–0·40	0·40–0·50	0·50–0·60	0·60–0·70
Males									
Series F, 15°–16° C.	100	66	3	21	10	—	—	—	—
Series C, 19°–22° C.	100	12	1	14	50	23	—	—	—
Series B, 25°–28° C.	152	—	—	—	11	87	2	—	—
Series E, 30°–32° C.	100	—	—	—	3	65	32	—	—
Series D, 25°–28° C., ⅛ sea-water	100	—	—	1	14	81	4	—	—
Series H, 25°–28° C., different stock	25	—	—	—	12	84	4	—	—
Females									
Series F, 15°–16° C.	100	48	4	25	23	—	—	—	—
Series C, 19°–22° C.	100	3	—	8	40	49	—	—	—
Series B, 25°–28° C.	100	—	—	—	1	85	14	—	—
Series E, 30°–32° C.	100	—	—	—	—	30	67	2	1
Series D, 25°–28° C., ⅛ sea-water	100	—	—	—	2	58	40	—	—
Series H, 25°–28° C., different stock	25	—	—	—	4	92	4	—	—

* Numbers of specimens expressed in percentages.

Tables XVI and XVII.: White band on hind tarsal segment IV

TABLE XVI.—*Aedes pseudoscutellaris*

Hind tarsal, Segment IV — *Greatest length of white band*

Ratio of white band to total length of segment*

	Number of specimens	0·50–0·55	0·55–0·60	0·60–0·65	0·65–0·70	0·70–0·75	0·75–0·80	0·80–0·85	0·85–0·90
Males									
Series F, 15°–16° C.	100	2	12	64	21	1	—	—	—
Series C, 19°–22° C.	100	—	5	33	48	13	1	—	—
Series B, 25°–28° C.	152	—	3	16	51	29	1	—	—
Series E, 30°–32° C.	100	—	—	1	15	57	24	2	1
Series D, 25°–28° C., ⅛ sea-water	100	—	—	2	20	52	24	1	1
Series H, 25°–28° C., different stock	25	—	—	4	56	36	4	—	—
Females									
Series F, 15°–16°c.	100	—	13	40	40	7	—	—	—
Series C, 19°–22° C.	100	—	1	14	65	19	1	—	—
Series B, 25°–28° C.	100	—	—	3	31	51	15	—	—
Series E, 30°–32° C.	100	—	—	1	4	36	48	9	2
Series D, 25°–28° C., ⅛ sea-water	100	—	—	—	5	44	44	6	1
Series H, 25°–28° C., different stock	25	—	—	—	28	56	16	—	—

* Numbers of specimens expressed in percentages.

TABLE XVII.—*Aedes pseudoscutellaris*

Hind tarsal, Segment IV	Number of specimens	*Least length of white band* Ratio of white band to total length of segment								
		0	0·01–0·10	0·10–0·20	0·20–0·30	0·30–0·40	0·40–0·50	0·50–0·60	0·60–0·70	0·70–0·80
Males										
Series F, 15°–16° C.	100	75	1	7	13	3	1	—	—	—
Series C, 19°–22° C.	100	6	—	5	6	18	44	21	—	—
Series B, 25°–28° C.	152	—	—	—	—	2	22	65	11	—
Series E, 30°–32° C.	100	—	—	—	—	1	—	60	39	—
Series D, 25°–28° C., ⅓ sea-water	100	—	—	—	—	2	17	73	8	—
Series H, 25°–28° C., different stock	25	—	—	—	—	—	40	60	—	—
Females										
Series F, 15°–16° C.	100	50	1	5	14	16	14	—	—	—
Series C, 19°–22° C.	100	1	—	—	2	5	43	48	1	—
Series B, 25°–28° C.	100	—	—	—	—	—	5	61	34	—
Series E, 30°–32° C.	100	—	—	—	—	1	—	21	72	6
Series D, 25°–28° C., ⅓ sea-water	100	—	—	—	—	—	3	39	58	—
Series H, 25°–28° C., different Stock	25	—	—	—	—	—	24	52	24	—

* Numbers of specimens expressed in percentages.

The greatest and least length of the band is affected by temperature similarly to the bands of the preceding segments. Specimens reared in ⅓ sea-water show some increase in white scaling, though this is not very marked in the least length of the band of the males. Series H is not greatly different from the original stock. The bands are longer, by both measurements, in females than in males of the same series. A high proportion of specimens reared at 15°–16° C. have the bands completely interrupted.

In *pseudoscutellaris* this segment is all white above, but occasionally has one or two dark scales at the base on its under side ; these seldom form any obvious interruption to the white scaling. Their presence was noted, and if they extended an appreciable distance along the segment, an estimate of this was made but no exact measurement.

The table records the percentages of specimens in which dark scales were present and also the percentage (of the total number of specimens) in which there was an observable interruption to the white scaling by a dark line beneath. The length of the dark line was measured from the base of the segment ; occasional dark scales at the tip were ignored. The categories are unequal and, except for total interruption, approximate.

Above 22° C. there is no great difference between the series though females at 25°–28° C. tend to have dark scales more often than those at 30°–32° C. or in ⅓ sea-water ; males from Series H have them more often than those of the original stock, but females do not differ. However, none of these series show any appreciable interruption by dark scales.

Table XVIII : Dark scaling on hind tarsal segment V

TABLE XVIII.—*Aedes pseudoscutellaris*

Hind tarsal, Segment V			*Amount of dark scaling beneath*		
		Dark scales*	Ratio of dark line to total length of segment*		
	Number of specimens	Absent	Present	0·25–0·50	0·50–0·99	1·00
Males						
Series F, 15°–16° C.	100	4	96	51	12	12
Series C, 19°–22° C.	100	39	61	2	1	—
Series B, 25°–28° C.	152	99	1	—	—	—
Series E, 30°–32° C.	99	94	6	—	—	—
Series D, 25°–28° C., ½ sea-water	100	92	8	—	—	—
Series H, 25°–28° C., different stock	25	72	28	—	—	—
Females						
Series F, 15°–16° C.	100	10	90	20	3	2
Series C, 19°–22° C.	100	60	40	—	—	—
Series B, 25°–28° C.	100	89	11	—	—	—
Series E, 30°–32° C.	100	99	1	—	—	—
Series D, 25°–28° C., ½ sea-water	100	99	1	—	—	—
Series H, 25°–28° C., different stock	25	88	12	—	—	—

* Number of specimens expressed in percentages.

(h) Table XIX.—Distance between lateral patches on tergites V and VI

TABLE XIX.—*Aedes pseudoscutellaris*

Abdominal tergites V and VI			*Horizontal distance between lateral white patches*			
	Tergite V			Tergite VI		
		Distance between patches*			Distance between patches*	
	Number of individuals	1–4 scales	5 or more scales	Number of individuals	1–4 scales	5 or more scales
Males						
Series F, 15°–16° C.	100	2	98	100	—	100
Series C, 19°–22° C.	100	2	98	100	2	98
Series B, 25°–28° C.	148	3	97	144	2	98
Series E, 30°–32° C.	100	8	92	100	8	92
Series D, 25°–28° C., ½ sea-water	100	4	96	100	3	97
Series H, 25°–28° C., different stock	25	9	91	25	12	88
Females						
Series F, 15°–16° C.	100	—	100	100	—	100
Series C, 19°–22° C.	100	—	100	100	—	100
Series B, 25°–28° C.	100	—	100	100	—	100
Series E, 30°–32° C.	100	1	99	100	3	97
Series D, 25°–28° C., ½ sea-water	100	—	100	100	2	98
Series H, 25°–28° C., different stock	25	—	100	25	4	96

* Numbers of specimens expressed in percentages.

At 19°–22° C. there is a marked increase in the number of specimens with dark scales and a few males have a measureable dark line; at 15°–16° few specimens are without dark scales and a notable proportion, particularly of males, have an incomplete dark line beneath, while in a few the interruption is complete.

Tergites V and VI were selected for the study of variation in abdominal markings as in all members of *scutellaris* subgroup the characteristic pattern of the species is most frequently found on one or both of these segments. In order to discover whether there was any tendency under different treatments for the lateral patches of *pseudoscutellaris* to extend and form a complete transverse band, the greatest horizontal distance between the lateral white scales was measured. Where the white scales were confined to continuous patches this is the distance between the patches, but in many cases beyond the tip of the continuous marking (i.e., towards the mid line) there were one or two isolated white scales.

Since the upper surface of the tergite is curved to a variable extent the measurement actually represents the chord of the arc, but the difference would be unimportant.

Measurements were made with a micrometer, 38 divisions of which equalled 1 mm. It was frequently observed that single scales measured in width approximately one of these divisions. The distances have therefore been expressed in the table as number of scales, in order that they may be easily interpretable. For evaluation of the results a distance of 4 or less was taken to represent a tendency to form a complete band (a condition comparable with the dotted bands of *riversi*, *horrescens* and *tongae*), but in no case was a complete band observed.

The table shows that there is very little tendency to form complete bands and this is scarcely affected by different treatments though there is some increase in white scaling at 30°–32° C., and males of all series show a little more white scaling than females; males of the different stock resemble those bred at 30°–32° C.

(*i*) Table XX: Specialized setae on the basal lobe

TABLE XX.—*Aedes pseudoscutellaris*

Basal lobe of coxite of male	Number of specimens	Number of lobes	*Number of specialized setae* Number of specialized setae*				
			2	3	4	5	6
Series F, 15°–16° C.	25	50	2	16	46	30	6
Series C, 19°–22° C.	25	50	—	20	54	24	2
Series B, 25°–28° C.	25	50	—	28	54	18	—
Series E, 30°–32° C.	25	50	2	22	52	20	4
Series D, 25°–28° C., ⅛ sea-water	25	50	2	14	50	26	8
Series H, 25°–28° C., different stock	10	20	—	35	60	5	—

* Number of lobes expressed in percentages.

The specialized setae on the basal lobe of the coxite are of particular interest as they are the most important character by which *pseudoscutellaris* is distinguished from *polynesiensis* (in which they are absent). Large variations in the number of

these would cast considerable doubt on their value in identification and delimitation of species.

As already recounted, the basal lobe was mounted in lateral view (see Fig. 5). The specialized setae are broad and well defined, but at the distal end of the row there may be one or two more slender setae which appear slightly flattened and it is often difficult to decide whether these should be included in the count or not. In order to avoid as far as possible any differences between series due to different interpretations of such setae at different times, a slide of genitalia mounts (2 or 3 per slide) was examined from each series in turn.

The results are shown in Table XX. They have been examined statistically and the difference between the series are not significant.

It may be added that although no records were made, there appeared also to be very little variation in the arrangement of the non-specialized setae on the basal lobe. An occasional specimen has a scale amongst the setae towards the tip, but this is an aberration that occurs also in *polynesiensis* (see Fig. 7).

(5) *Summary of Experimental Results*

The following is a summary of the results obtained from a biometrical study of specimens of *Aedes pseudoscutellaris* reared under controlled conditions in which one factor of the larval environment was varied.

1. Size of adults decreases with increase in temperature or salinity of the larval environment.

2. In general, the amount of white scaling increases with rise in temperature; conversely the amount of dark scaling increases with fall in temperature. The reverse has not been observed but some characters are not affected.

3. Increase in temperature effects an increase in white scaling in the following positions: under side of proboscis; anterolateral margin of scutum; fore and mid tarsal segments III, fore tarsals IV–V, hind tarsals I–IV; abdominal tergites V and VI. Many of these characters follow a parallel gradient to the temperature; others are affected only at low or at high temperatures, or to different degrees in the two sexes. The dark ventral line on the hind femur increases in extent with decrease in temperature.

4. A larval environment of $\frac{1}{3}$ sea-water effects a decrease in white scaling under the proboscis of males; and an increase in white scaling on fore tarsal segments IV–V and hind tarsal II of females and on hind tarsals III–IV of both sexes. Other scale characters are apparently not affected.

5. The extent of white scaling on either side of the prescutellar bare area and the length of the anterior white streak on the hind femur do not appear to vary in relation to larval environment.

6. Males tend to have more white scaling on the under side of proboscis, anterolateral margin of scutum and lateral patches of abdominal tergites, than do females reared in the same conditions.

7. Females tend to have more white scaling on fore tarsal segments III–V, mid tarsal III and hind tarsals III–IV, than do males reared in the same conditions.

8. A white streak under the proboscis may be absent or variable in one stock and well developed in another stock of the same species.

9. The characteristic white scaling on the anterolateral margin of scutum is retained in varied environments.

10. Although the greatest lengths of white bands on the hind tarsi vary with larval environment, the total variation is insufficient to affect seriously their use as taxonomic characters.

11. Low temperatures may produce partial or complete interruption of the white bands on the hind tarsal segments.

12. The characteristic markings of the abdominal tergites are retained in varied environments.

13. The number of specialized setae on the basal lobe of the male coxite is not varied significantly by alteration of larval environment.

(6) *Conclusions*

It would be unsafe to regard the results of these studies on a small population as applicable to *pseudoscutellaris* as a whole, let alone to other species of the *scutellaris* subgroup. Nevertheless, they do support the specific status given to members of the *scutellaris* subgroup by showing that, although currently accepted diagnostic characters can be varied by environmental conditions, with few exceptions the range of variation is not of the same magnitude as the differences between species in the same character. They also show that these characters remain relatively constant through numerous generations. In particular, the lack of variation in the basal lobe of the male coxite is evidence of the value of this structure in defining species.

The experiments suggest that two characters should be used with some caution for delimiting species since *pseudoscutellaris* can exhibit both extremes of their development. Complete interruption to the white bands on hind tarsal segments II–IV can be produced by low temperatures of larval environment. The presence or absence of a white streak under the proboscis may be due to differences in hereditary constitution, but there is also, in males, a greater tendency for a streak to be present in specimens reared at higher temperatures.

It is possible that in other species of the *scutellaris* subgroup, these characters may be genetically fixed. In this connection it may be noted that Waddington (1952) has shown experimentally, in *Drosophila melanogaster*, that in the course of selection, a genetic constitution may be synthesized, which under normal conditions produces the same effect as was originally found only as a response to the stimulus of an abnormal environment.

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